



No direction specific costs in trans-saccadic memory

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ABSTRACT

Even though we frequently execute saccades, we perceive the external world as coherent and stable. An important mechanism of trans-saccadic perception is spatial remapping: the process of updating information across eye movements. Previous studies have indicated a right hemispheric dominance for spatial remapping, which has been proposed to translate into enhanced trans-saccadic memory for locations that are remapped into the right compared to the left hemisphere in healthy participants. Previous study designs suffered from several limitations, however (i.e. multiple eye movements had to be made instead of one, fixations were not controlled for, and ceiling effects were likely present). We therefore compared accuracy of trans-saccadic memory for central items after left- versus rightward eye movements, and secondary, for items that were remapped within the left versus right visual field. Participants memorized the location of a briefly presented item, made one saccade, and subsequently decided in what direction the item had shifted. We used a staircase to adjust task difficulty. Bayesian repeated measures ANOVAs were used to compare between left versus right eye movements and items in the left versus right visual field. We found most evidence against directional differences in trans-saccadic memory ($BF_{10} = 0.23$). We found some evidence suggestive of enhanced trans-saccadic memory for items that were remapped within the left compared to the right visual field ($BF_{10} = 4.00$). The latter result could be explained by a leftward spatial attention bias. As such, the hypothesized right hemispheric dominance for spatial remapping does not result in asymmetric trans-saccadic memory capacities in healthy participants.

1. Introduction

Even though we frequently execute saccades, we perceive the external world as coherent and being rich in detail, despite the discontinuous manner in which it is visually processed. This is known as trans-saccadic perception (Prime et al., 2011). There are two central processes in trans-saccadic perception: the visual information must be stored in memory across saccades (i.e. trans-saccadic memory) and the visual information must be spatially updated. A mechanism that probably underlies trans-saccadic perception is ‘spatial remapping’.

As detailed information is processed only over a few degrees of visual angle at the fovea, we continuously make eye movements. The representation of the visual field in early occipital areas is retinotopic, meaning that the representation is centred on the instantaneous eye position. When we make eye movements, this representation is overwritten by a new one, centred on the new eye position. Thus, across eye movements, the old information must be updated into the new gaze-centred reference frame to remain accurate. Spatial remapping is the

process of integrating the content of individual fixations over space and time into a stable, internal representation of the environment (Bays and Husain, 2007; Pisella et al., 2011; Pisella and Mattingley, 2004).

Studies in monkeys (Duhamel et al., 1992) suggest that neurons in the posterior parietal cortex (PPC) play a role in spatial remapping. The receptive fields of these neurons change *before* an eye movement, and neurons respond when an eye movement brings a previously flashed location into the receptive field (i.e. a memory trace; Colby and Goldberg, 1999; Duhamel et al., 1992). Human functional neuroimaging results also suggest that activity in the PPC is associated with encoding and updating information in a gaze-centred reference frame (Medendorp et al., 2003; Merriam et al., 2003). In particular the *right* PPC seems to play a dominant role in this mechanism: TMS over the right PPC disrupts trans-saccadic memory in humans (Chang and Ro, 2007; Morris et al., 2007; Prime et al., 2008; Van Donkelaar and Müri, 2002; van Koningsbruggen et al., 2010), whereas TMS over the left PPC has no effect (Prime et al., 2008; van Koningsbruggen et al., 2010), and more severe trans-saccadic memory deficits are observed after lesions in

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the right compared to the left PPC (Heide and Kömpf, 1998; Pisella et al., 2011; Sapir, et al., 2004). Activity in the PPC could, therefore, possibly contribute to trans-saccadic memory at a cognitive/perceptual level. Neurons demonstrating spatial remapping have, however, also been found in other brain areas, such as the macaque analogue of the human intraparietal sulcus (IPS), the frontal eye fields (FEF), and area V4 (e.g. Andersen et al., 1990; Neupane et al., 2016; Umeno and Goldberg, 2001; Wang et al., 2016).

Disturbed spatial remapping could explain some of the symptoms of visuospatial neglect (Pisella and Mattingley, 2004), a disorder in lateralized attention. Visuospatial neglect is accompanied by non-lateralized deficits, such as revisiting behaviour (Mannan et al., 2005) and disorganized search (Butler et al., 2009; Rabuffetti et al., 2012; Ten Brink et al., 2016). Vuilleumier et al. (2007) hypothesized that impairments in spatial remapping after right hemisphere lesions result in the loss of location information specifically when the eyes move to the ipsilesional, right direction. They found this in patients with right brain damage and visuospatial neglect. For a location that is initially encoded at fixation, an eye movement towards the right should remap this location *leftwards* in gaze-centric terms. The information would then be remapped into neurons of the right hemisphere. If the neurons that process the leftward locations within gaze-centric maps are damaged, such remapping might be disturbed. The same deficit was found in patients with right hemisphere damage and constructional apraxia (i.e. the inability to copy simple figures; Russell et al., 2010).

Vasquez and Danckert (2008) hypothesized that, if remapping relies mostly on right hemispheric activities, the opposite pattern from the patient studies should be observed in healthy participants. Indeed, they observed a greater cost on trans-saccadic memory accuracy after remapping items into the right visual space (following a leftward eye movement) compared to the left visual space (following a rightward eye movement) in healthy participants. Vasquez and Danckert (2008) explained their results by the well-known right hemisphere dominance for spatial processes. For instance, right hemisphere mechanisms have been shown to be more efficient for spatial attention, attention in general, and processing exact metric spatial information (i.e. location memory) compared to the left hemisphere (Vasquez and Danckert, 2008). It is interesting to note that such an asymmetry was not observed in the healthy participants who served as a control group in the patient studies (Russell et al., 2010; Vuilleumier et al., 2007). This could be explained by a ceiling effect, as task difficulty was the same for patients and healthy participants. This is reflected in the high to perfect scores that were obtained in the control groups.

The designs of these studies (Russell et al., 2010; Vasquez and Danckert, 2008; Vuilleumier et al., 2007) suffered from several limitations, however. Most important, in none of the studies fixations were controlled for. Related to this, in the patient studies, two eye movements had to be made instead of one (left-right or right-left; Russell et al., 2010; Vuilleumier et al., 2007), which makes it impossible to disentangle which eye movement direction (i.e. leftward or rightward) caused the observed trans-saccadic memory deficit. Because eye movements were made in both directions, potential differences between gaze directions could have cancelled each other out, which could explain the null findings in the control groups.

Furthermore, in the studies of Vasquez and Danckert (2008) and Vuilleumier et al. (2007), no differentiation was made between ‘intra-hemispheric’ and ‘inter-hemispheric’ remapping. For a memory item that is presented in one visual field, it is expected that the opposite hemisphere processes this item. If, after an eye movement is made, this item is located in the same visual field, the *same* hemisphere would process the item (i.e. intra-hemispheric remapping). In case the eye movement would cause the item to shift between the visual fields, remapping would have to take place *between* hemispheres (i.e. inter-hemispheric remapping; Parks and Corballis, 2010). In both left- and rightward gaze conditions, memory items could be presented in the left or right visual field. Eye movements had to be made away from or

towards the item location. Thus, in each condition, both hemispheres were involved in the spatial remapping process, and, therefore, no conclusions can be drawn regarding hemispheric dominance.

Our main aim was to further investigate whether healthy participants show a decrease in trans-saccadic memory when a memory item in the centre of the screen is remapped *towards* the left compared to the right hemisphere, by using a single-eye movement design. As we expected the differences between sides to be small in healthy participants, and to avoid ceiling effects which were possibly observed in other studies (Russell et al., 2010; Vuilleumier et al., 2007), a staircase was used throughout the experiment to adapt task difficulty to the participant. Vasquez and Danckert (2008) aimed to measure spatial working memory by presenting one target among non-targets, and participants were instructed to memorize the location of the target stimulus. In the studies of Russell et al. (2010) and Vuilleumier et al. (2007), no non-target stimuli were used. To compare our results with those of previous studies, we administered the task either with and without non-targets. Based on the study of Vasquez and Danckert (2008), we expected better trans-saccadic memory accuracy after rightward compared to leftward eye movements. A secondary aim was to investigate whether trans-saccadic memory accuracy would be enhanced for items presented and remapped *within* the left compared to the right visual field. We expected better performance for items that were presented in the left compared to the right visual field.

2. Methods

2.1. Participants

We aimed to include at least 30 participants per task (i.e. with and without non-targets), or stop when a Bayes factor of 6 was reached for the main analysis (i.e. the comparison between trans-saccadic memory after leftward versus rightward gaze shifts). As we did not reach the Bayes factor of 6, we tested 63 participants in total. The participants (mean age = 22.14, SD = 2.06 years; 54% female) took part in the study for either money or course credits. All reported normal or corrected-to-normal visual acuity and no history of neurological conditions. The experiment was performed in accordance with the Declaration of Helsinki. Procedures were approved by the Ethical Review Committee (Faculty of Social Sciences, Utrecht University). All participants gave written informed consent.

2.2. Apparatus, stimuli, procedure, and design

Participants were seated in a light and sound attenuated room at 70 cm from a computer monitor (60.7 × 35 cm). Their head was stabilized using a chin rest. Monocular eye movement data was collected at 1000 Hz using an SR Research EyeLink 1000 eye tracker, located at 600 mm from the eye. Participants were tested having both eyes open, and the left eye was monitored. We used nine-point calibrations at the beginning of the experiment and between trials when necessary. Experimental tasks were programmed using MATLAB (version R2015a).

Stimuli were presented against a black background. Participants were instructed to fixate a central cross (0.5°, white, luminance 33.3 cd/m²). From the moment of fixation, there was a random delay of 500 to 1000 ms where after a memory item (filled circle, Ø1°, red or blue, luminance 3.20 cd/m² and 3.77 cd/m² respectively) appeared for 250 ms. The item was presented at a random distance in between 5° and 8° either above, below, left, or right from fixation, depending on the experimental condition. In the “gaze left/gaze right” conditions, the item was presented either above or below fixation where after participants had to make a leftward (“gaze left”) or rightward (“gaze right”) eye movement. In the “item left/item right” conditions, the item was presented either left (“item left”) or right (“item right”) from fixation, after which participants had to make an eye movement up- or

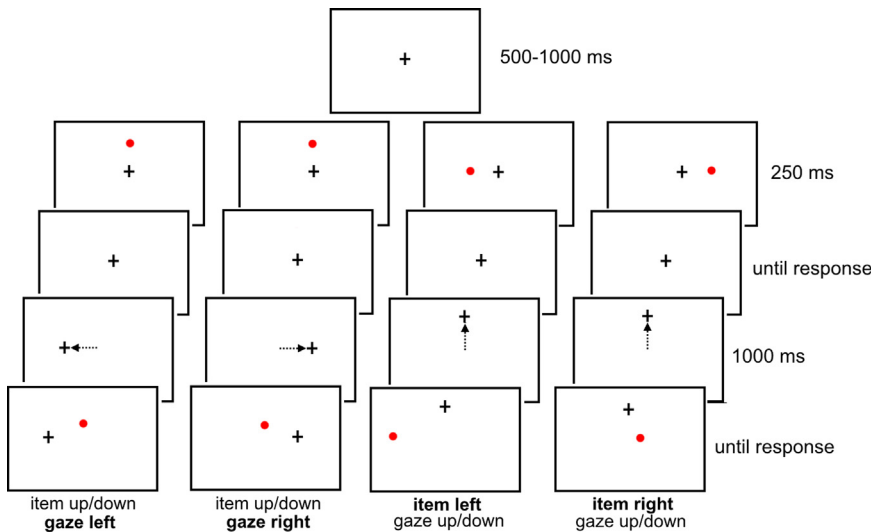


Fig. 1. Illustrative sequences of events for the four different conditions in the task without non-targets. From fixation (upper panel), a random delay of 500–1000 ms was introduced. Then, a memory item appeared for 250 ms. Participants had to name the colour of the item and memorize its location. After the colour response was given, the fixation cross shifted. When participants fixated the cross again, there was a delay of 1000 ms. A probe appeared and remained onscreen until participants indicated in which direction the probe had shifted relative to the memory item.

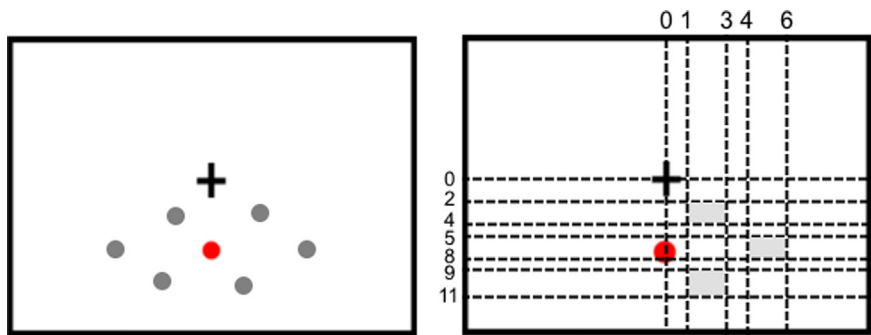


Fig. 2. In the left panel, an example of a trial with non-targets in the “gaze left/gaze right” conditions is depicted. Note that these elements are only presented together with the memory item appearance and not with the probe. In the right panel, the areas in which the elements could be presented are marked grey. The numbers depict the ranges of the element locations, expressed as visual degrees from fixation. Non-targets were presented at random locations in the grey areas on the right, and in mirrored areas on the left (not depicted). The element locations were rotated 90° in the “item left/item right” conditions (i.e. elements were presented above and below the memory item).

downward (Fig. 1). Of 63 participants, 33 performed the task without non-targets and 30 with non-targets. In the task with non-targets, six stimuli (grey filled circle, Ø1°, luminance 4.95 cd/m²) were presented simultaneously with the memory item at random locations within predefined ranges (Fig. 2). Participants had to name the colour of the memory item, so we could verify whether the item had been identified. Although this was mostly important in the task with the non-targets, we wanted to be able to compare both tasks (with and without non-targets), and minimize other differences between them. Therefore, participants had to name the colour of the target in all conditions. The experimenter entered the answer using the keyboard (‘r’ for red and ‘b’ for blue).

Subsequently, the fixation cross shifted 6° towards the left or right in the “gaze left/gaze right” conditions, and up or down in the “item left/item right” conditions. After the fixation cross shifted position, the trial continued when participants re-fixated the cross. When participants re-fixated the fixation cross, there was a 1000 ms delay, after which a probe appeared (same colour and size as the memory item) and remained on screen. The probe was shifted relative to the memory item, either up or down in the “gaze left/gaze right” conditions or left or right in the “item left/item right” conditions. Spatial remapping is based upon an efferent motor copy of the eye movement signal and can lead to spatial errors. These errors build up along the axis of the saccades. In other words, an eye movement along the horizontal axis makes it more difficult to detect displacements along the same (horizontal) axis compared with the vertical axis (Peterson et al., 2018). The task lay-out was, therefore, rotated 90 degrees so that the direction of the displacement was always along a different axis than the direction of the eye movement and conditions were as similar as possible.

Participants had to report the direction of the shift. We wanted to avoid a motor bias in the response by having to reach leftward or

rightward when giving the response. As we were not interested in response times, we choose to let people respond verbally. The experimenter entered the answer using the keyboard (using arrow keys).

The size of the shift between the memory item and probe was defined based on a staircase algorithm. We used Accelerated Stochastic Approximation (ASA), a non-parametric adaptive procedure that, by quickly reducing step size, rapidly converges to any accuracy level (Kesten, 1958). In the first trial, the probe always shifted 5° relative to the memory item. The ASA staircase gradually decreases step size in two ways. In the second and third trial, the size of the shift between the memory item and probe on the next trial (d_{k+1}) was given by:

$$d_{k+1} = d_k - \frac{3}{k}(Z_k - 0.8)$$

where d_k is the distance used in the current trial, 3 is the staircase constant to determine the shift in degrees of visual angle between the memory item and probe, k is the trial number, Z_k is 1 when a correct response was provided in the current trial or 0 when an incorrect response was provided, and 0.8 is the desired accuracy level. For trial $n > 3$ step size changes as a function of the number of changes in ‘response category’ (i.e. switch trials from consecutive correct to incorrect, or vice versa):

$$d_{k+1} = d_k - \frac{3}{2 + m_{switch}}(Z_k - 0.8), \quad k > 3$$

where m_{switch} is the number of switch trials. The minimum and maximum step sizes were set at 0.1° and 5° respectively. Ideally, the final threshold estimate is taken from the staircase estimates when the step size reaches a predefined lower limit. However, this means that the duration of the task is undefined. As there was no criterion to decide whether the staircase converged, we collected as many trials as possible within 1 hour, resulting in 64 to 80 trials per condition. Note that for

each condition (i.e. gaze left, gaze right, item left, item right), a separate staircase procedure was used throughout the experiment. Per condition, the estimated distance in visual degrees at which participants were able to detect the direction of the probe shift in 80% of trials (“discrimination threshold”) was computed based on the final 1/3 of trials. Later trials put more weight in the equation based on a linear relationship, the sum of the weights was 1. Thus, the last trial was the most influential single trial in our threshold computation. We used the weighted average for two reasons. First, we could not include all trials (see below for exclusion criteria of trials) and had a time constraint on the experiment, which does not guarantee that the staircase converged. Second, we put a constraint on the minimum step size to keep subjects engaged in the experiment. The calculated step size could theoretically be smaller than the minimal physical step size on our screen, effectively resulting in a step size of 0.

The four conditions were divided into two block types (i.e. “gaze left/gaze right” and “item left/item right”) that alternated throughout the experiment. The direction of the fixation shift, colour of the memory item, initial location of the memory item, and direction of the probe shift were counterbalanced across the conditions and randomized within blocks. The order of the block types was randomized across participants. One block consisted of 32 experimental trials. At the start of each block, two additional (randomly picked) trials were presented. Responses provided in these trials were not included in the staircase algorithm to make sure that potential costs of switching between blocks did not affect the outcome. The shift size in these trials was based on the previous distance from the staircase procedure of the given condition. Note that per condition, the staircase procedure continued from the previous block throughout the experiment. Prior to the experiment, practice trials were provided until the participant was able to perform the task.

Participants were instructed to fixate the cross throughout the task, and make no eye movements towards the memory item or probe. Eye movements within 2° from a stimulus (i.e. either the fixation cross, memory item, or probe) were considered fixations at this stimulus and were detected on-line by the experimental program or manually by the experimenter. A trial was aborted and not included in the staircase procedure when the memory item or probe was fixated or when the colour of the memory item was incorrectly named. These exclusion criteria led to a mean loss of 3.61% of trials (range: 3.12% to 4.35% across the four different conditions), mainly due to accidental fixations at the memory item. After exclusion, a median of 63 trials was available per condition (range: 48–80 trials). Per participant, we kept the same number of trials per condition to avoid possible outcome differences due to unequal amount of trials. Thus, the condition with the lowest number of trials was indicative of the number of trials to maintain for each condition.

We did not include a “no-gaze” condition, as the execution of eye movements involves visuospatial working memory (Peterson et al., 2018; Van der Stigchel and Hollingworth, 2018). Remembering a spatial location and making an eye movement can be considered a dual-task. Any differences between a fixation and a no-fixation condition could therefore also be attributed to a general dual-task effect.

2.3. Data analysis

2.3.1. Eye movements

As we used a staircase algorithm, we excluded invalid trials on-line as it was not possible to exclude trials after the experiment had finished. We checked the quality of the eye movement data in retrospect (without excluding trials based on this quality check). We analysed how well participants had fixated the fixation cross throughout the task, separately for the first half of the trial (i.e. from the appearance of the memory item until the fixation shift) and the second half of the trial (i.e. from the appearance of the memory probe until the answer was provided). We used the marks that were provided by the EyeLink on-line

parser (SR Research Ltd., Mississauga, Ontario, Canada, n.d.) to distinguish between the onset and end of fixations, saccades, and blinks. Based on all fixations that (partly) occurred within the predefined periods, we computed the average deviation from the fixation cross on both the x-axis and y-axis and the percentage of fixations that were more than 3° away from the fixation cross. In addition, for each condition, we computed the average of participant’s median latency and accuracy (i.e. the absolute distance between the endpoint and the shifted fixation cross) of the gaze shift, defined as the first eye movement of > 3° after the fixation cross had shifted. Bayesian paired-samples *t*-tests (two-tailed) were used to compare saccade latency and accuracy between the gaze left versus gaze right, and item left versus item right conditions.

2.3.2. Accuracy of trans-saccadic memory

We compared the discrimination threshold between the gaze left and gaze right conditions and between the item left and item right conditions using Bayesian repeated measures ANOVAs with ‘task’ as between subject factor (i.e. with or without non-targets). The Bayes factor indicates whether there is more evidence in favour of one hypothesis over the other, based on the observed data. With frequentist analysis, a *p*-value is the probability of obtaining results at least as extreme as those observed given that H_0 is true (Wagenmakers et al., 2018). The *p*-value does not take into account whether the alternative hypothesis is more likely or not, which is what we were interested in. We report Bayes Factors (*BF*), using the Savage-Dickey density ratio method, which can be interpreted as the weight of evidence for one hypothesis over another (Wagenmakers et al., 2010; Wagenmakers et al., 2018). Specifically, we report BF_{10} , the evidence in favour of the alternative hypothesis. Note that BF_{01} , the evidence in favour of the null hypothesis, is related to this value and can be computed by the following formula: $BF_{01} = 1 / BF_{10}$. Kass and Raftery (1995) have provided guidelines to interpret the *BF* as weight of evidence. A *BF* of 1 to 3 is described as providing evidence that is ‘not worth more than a bare mention’. A *BF* of 3 to 20 provides ‘positive’ evidence, 20 to 100 ‘strong’ evidence, and above 100 ‘very strong’ evidence. We used the default settings for ANOVA designs to set the prior distribution (Rouder et al., 2012). Data was analysed using JASP version 0.9 (JASP Team, 2018; Wagenmakers et al., 2018). The Bayes factor of the interaction effect was computed by selecting the option ‘effects across matched models’ in JASP.

3. Results

3.1. Eye movements

On-line eye movement measurements were used for all 63 participants. 52 Full eye movement datasets were also analysed offline to evaluate quality of the eye movement data in retrospect. Note that we did not exclude additional trials based on this evaluation, as task difficulty was adjusted based on trials that were included on-line. Due to recording problems, 3 eye movement datasets were not available offline, and 8 only partially. We analysed the partial eye movement datasets similar to the complete datasets. Note that this only regards the offline eye movement data, the other data (i.e. on-line eye movement recordings necessary to exclude trials, and the recordings of responses to compute the discrimination threshold) was fully available for all participants.

Participants deviated on average 0.24° (SD = 0.44°) on the x-axis and -0.22° (SD = 0.57°) on the y-axis from the fixation cross before the fixation cross shifted (first half), and 0.23° (SD = 0.62°) on the x-axis and -0.15° (SD = 0.62°) on the y-axis after the fixation cross had shifted (second half). 4.52% (SD = 4.57%) of all fixations in the first half, and 4.81% (SD = 5.62%) of all fixations in the second half was more than 3° away from the fixation cross. This indicates that participants mostly fixated the fixation cross throughout the task, and only one eye

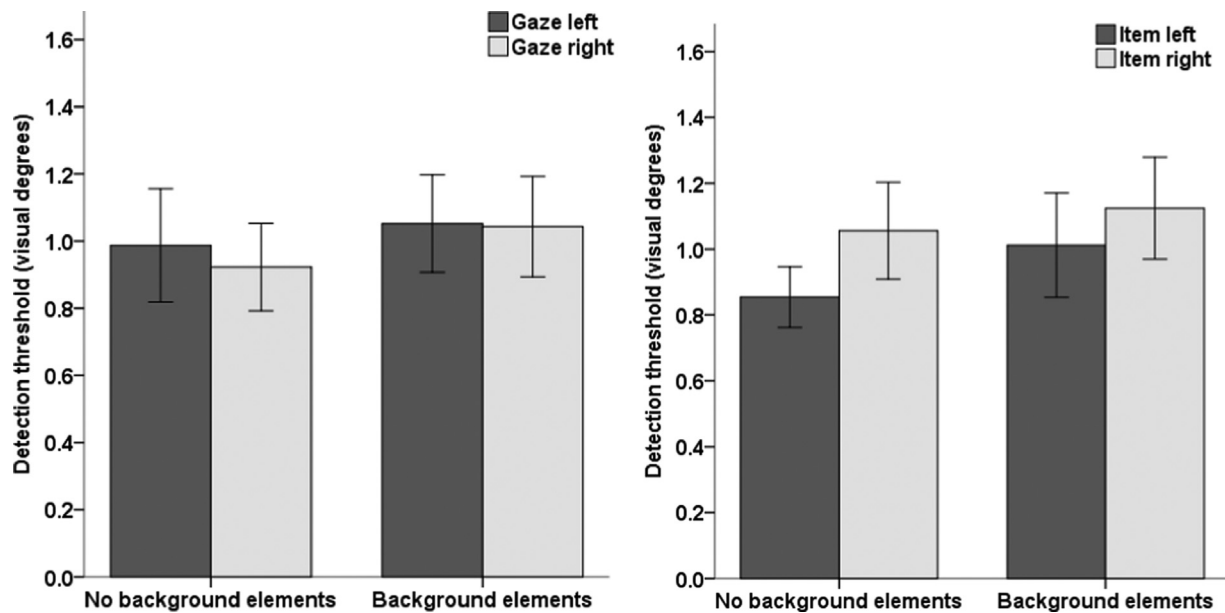


Fig. 3. Mean discrimination threshold (in visual degrees) split for task and condition. Error bars depict 95% confidence intervals.

movement was made.

There was no difference in saccade latency between the gaze left (192 ms, SD = 44 ms) and the gaze right conditions (190 ms, SD = 41 ms; $BF_{10} = 0.15$), and between the item left (205 ms, SD = 32 ms) and item right conditions (204 ms, SD = 31 ms; $BF_{10} = 0.17$). Note that no comparison was made between gaze up versus gaze down, as we were only interested in differences between the item left versus item right conditions.

The accuracy of the gaze shifts (i.e. the absolute distance between the saccade endpoint and fixation cross) was higher in the gaze left (1.19°, SD = 0.46°) than in the gaze right condition (1.38°, SD = 0.55°; $BF_{10} = 24.42$). Thus, participants made more accurate eye movements to the fixation cross in the left visual field than to the fixation cross in the right visual field. There was no difference in eye movement accuracy between the item left (1.42°, SD = 0.45°) and the item right condition (1.38°, SD = 0.38°; $BF_{10} = 0.37$), in which eye movements were directed either upward or downward.

3.2. Accuracy of trans-saccadic memory

Mean discrimination thresholds (in visual degrees) are depicted in Fig. 3. The Bayesian Repeated Measures ANOVA output is depicted in Tables 1–4.

There was more evidence for the null hypothesis than the alternative hypothesis when comparing the gaze left versus gaze right conditions, $BF_{10} = 0.23$ ($BF_{01} = 4.35$). Thus, there was no difference in accuracy of trans-saccadic memory after leftward versus rightward eye movements. We found inconclusive results regarding the difference between tasks (i.e. with or without non-targets), although there was slightly more evidence against a difference $BF_{10} = 0.45$ ($BF_{01} = 2.22$).

Table 1
Model comparison for the “gaze left/gaze right” conditions.

Models	P(M)	P(M data)	BF _M	BF ₁₀	Error %
Null model (incl. subject)	0.200	0.551	4.899	1.000	
Gaze	0.200	0.127	0.583	0.231	1.122
Task	0.200	0.246	1.307	0.447	0.880
Gaze + Task	0.200	0.057	0.243	0.104	1.553
Gaze + Task + Gaze * Task	0.200	0.019	0.076	0.034	9.873

Note. All models include subject.

Table 2
Analysis of effects for the “gaze left/gaze right” conditions.

Effects	P(incl)	P(incl data)	BF Inclusion
Gaze	0.400	0.185	0.232
Task	0.400	0.304	0.448
Gaze * Task	0.200	0.019	0.325

Note. Compares models that contain the effect to equivalent models stripped of the effect. Higher-order interactions are excluded.

Table 3
Model comparison for the “item left/item right” conditions.

Models	P(M)	P(M data)	BF _M	BF ₁₀	Error %
Null model (incl. subject)	0.200	0.113	0.507	1.000	
Item	0.200	0.459	3.396	4.078	0.976
Task	0.200	0.065	0.278	0.576	1.838
Item + Task	0.200	0.276	1.522	2.448	1.787
Item + Task + Item * Task	0.200	0.088	0.385	0.779	4.441

Note. All models include subject.

Table 4
Analysis of effects for the “item left/item right” conditions.

Effects	P(incl)	P(incl data)	BF Inclusion
Item	0.400	0.735	4.140
Task	0.400	0.341	0.596
Item * Task	0.200	0.088	0.318

Note. Compares models that contain the effect to equivalent models stripped of the effect. Higher-order interactions are excluded.

There was no interaction effect between gaze direction and task, $BF_{10} = 0.33$ ($BF_{01} = 3.03$).

There was most evidence for the model that included the item left and item right conditions, $BF_{10} = 4.00$, which suggested more accurate trans-saccadic memory for items in the left versus the right visual field. The result regarding the effect of task, $BF_{10} = 0.58$ ($BF_{01} = 1.72$) was inconclusive. There was no interaction effect between item side and task, $BF_{10} = 0.32$ ($BF_{01} = 3.14$).

4. Discussion

We studied whether the proposed right hemispheric dominance for spatial remapping translates into enhanced trans-saccadic memory performance for locations that are remapped into the right compared to the left hemisphere. We found about 4 times more evidence for the null hypothesis than the alternative hypothesis, suggesting there is no difference in accuracy of trans-saccadic memory after leftward versus rightward eye movements. We found no strong evidence for differences between item sides, although there was about 4 times more evidence for enhanced trans-saccadic memory accuracy for items that were remapped within the left compared to the right visual field. We found inconclusive results regarding the effect of non-targets on trans-saccadic memory performance.

Our results contrast with those of Vasquez and Danckert (2008), who found better trans-saccadic memory accuracy after rightward compared to leftward eye movements. In their study, however, no dissociation was made based on initial item location (i.e. left or right). Thus, the situation in which an item appeared in the left visual field and had to be remapped within the same, left visual field, only occurred when a rightward eye movement had to be made. This fits with our trend of enhanced trans-saccadic memory accuracy for items that had to be remapped within the left versus the right visual field. The difference between studies regards the direction of the eye movement, which was rightward in the study of Vasquez and Danckert (2008) and up- or downward in our study. As we found no differences for trans-saccadic memory accuracy after leftward versus rightward eye movements for centrally presented items, the fact that Vasquez and Danckert (2008) found an effect cannot be explained by the difference between leftward versus rightward eye movements.

Our data suggests a trend of enhanced trans-saccadic memory accuracy for items in the left versus the right visual field. This could, instead of remapping differences, be due to a leftward bias of other visuospatial processes, such as spatial attention. Healthy participants tend to exhibit a (small) spatial attention bias towards the left. In eye tracking studies on free viewing of images and face perception there usually is an initial leftward bias in exploration (e.g. Butler and Harvey, 2005; Calen Walshe and Nuthmann, 2014; Mertens et al., 1993; Ossandon et al., 2014). In addition, when asked to bisect the middle of a line, healthy participants make small leftward errors (i.e. pseudo neglect; Bowers and Heilman, 1980; Jewell and McCourt, 2000). The cause of this leftward bias remains unresolved but could be due to hemispheric asymmetries in visuospatial attention (Bowers and Heilman, 1980; Jewell and McCourt, 2000). An alternative explanation is that the leftward bias is due to reading direction habits (Afsari et al., 2016). Spatial attention and spatial working memory are closely related processes: responses are faster for cued locations (Posner, 1980) and for locations that are maintained in spatial working memory (Awh et al., 1998), and location memory is impaired when attention is withdrawn during a delay (Awh et al., 1998; Johnson and Spencer, 2016). If attention is greater for the left compared to the right visual field, this could possibly explain the enhanced trans-saccadic memory accuracy for items that are presented left, regardless of whether an eye movement was made or not. Having said this, it should be stressed that this is just speculative and the evidence for enhanced performance for items in the left visual field was small.

One could argue that, if a leftward attention bias results in better trans-saccadic memory accuracy for items in the left compared to items in the right visual field (i.e. in the *item left/item right conditions*), this would also lead to enhanced performance for a central item that is remapped into the left visual field, thus, after making a rightward eye movement versus after making a leftward eye movement (i.e. in the *gaze left/gaze right conditions*). We did not find any differences between trans-saccadic memory accuracy after rightward versus leftward eye movements, however. In the current experiment, the memory item was only briefly shown (i.e. 250 ms), whereas the probe remained onscreen

until a response was given. Possibly, enhanced attention for the first, shorter presented memory item (i.e. when the memory item was presented in the left visual field) benefit trans-saccadic memory, whereas enhanced attention for the probe (i.e. when the probe was shown in the left visual field after a rightward eye movement was made) could not further improve trans-saccadic memory accuracy. Another explanation for the fact that we found no differences in the gaze left/gaze right conditions while we did see a bias in the item left/item right conditions, could be that asymmetries observed in pseudo neglect relate to hemispace (i.e. the left or right side relative to the body midline) rather than visual field (Bowers and Heilman, 1980; Bradshaw et al., 1983). As the memory item was always presented at a central position relative to the body midline in the gaze left/gaze right conditions, this could explain why no differences in trans-saccadic memory performance were found after a rightward compared to a leftward eye movement, as the item was remapped into the left visual field but not into the left hemispace. However, it is still unknown whether pseudo neglect relates to hemispace only, as this has been reported mainly for tactile tasks (Bowers and Heilman, 1980; Bradshaw et al., 1983) and discrepant findings have been reported for their visual counterparts (Jewell and McCourt, 2000).

Nevertheless, most likely, the right hemisphere is involved in spatial remapping of information in *both* the left and right visual fields. When the right PPC is functionally impaired (due to a virtual lesion induced by TMS or due to brain damage), trans-saccadic memory impairments can be expected independent of saccade direction, with most problems after rightward eye movements (i.e. when information is remapped into the left visual field). This is indeed reflected in the results of prior studies in which trans-saccadic memory accuracy was tested in patients with right PPC lesions or in healthy participants after applying TMS at the right PPC: some found direction specific impairments (Chang and Ro, 2007; Heide and Kömpf, 1998; Morris et al., 2007; Van Donkelaar and Müri, 2002), whereas other found general impairments (i.e. both after leftward and rightward saccades; Prime et al., 2008; Sapir et al., 2004; van Koningsbruggen et al., 2010). Contrary, in healthy participants, the right hemispheric dominance for spatial remapping would not necessarily be expressed as a behavioural difference between sides.

To conclude, we found no differences in trans-saccadic memory accuracy for items that were remapped following leftward versus rightward eye movements. There was a trend for enhanced trans-saccadic memory accuracy when items were presented within the left compared to the right visual field, which could be due to a leftward spatial attention bias. These findings do not necessarily contradict the hypothesis that the right hemisphere is dominant in spatial remapping, because the right hemisphere is most likely involved in remapping after both leftward and rightward saccades. Given that we used a sensitive staircase paradigm and applied Bayes statistics to compare our hypotheses, and no clear effect emerged, we argue that there are no alternative explanations for our null-finding other than the lack of a difference in trans-saccadic memory accuracy after leftward versus rightward eye movements.

CRedit authorship contribution statement

A.F. Ten Brink: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing - original draft, Visualization. **T.C.W. Nijboer:** Conceptualization, Writing - review & editing, Supervision. **J.H. Fabius:** Conceptualization, Methodology, Software, Formal analysis, Writing - review & editing. **S. Van der Stigchel:** Conceptualization, Methodology, Writing - review & editing, Supervision, Project administration, Funding acquisition.

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Declaration of interest

The authors declare that they have no conflict of interest.

References

- Afsari, Z., Ossandón, J.P., König, P., 2016. The dynamic effect of reading direction habit on spatial asymmetry of image perception. *J. Vis.* 16 (11), 8. <https://doi.org/10.1167/16.11.8>.
- Andersen, R., Bracewell, R., Barash, S., Gnadt, J., Fogassi, L., 1990. Eye position effects on visual, memory, and saccade-related activity in areas LIP and 7a of macaque. *J. Neurosci.* 10 (4), 1176–1196. <https://doi.org/10.1523/JNEUROSCI.10-04-01176.1990>.
- Awh, E., Jonides, J., Reuter-Lorenz, P.A., 1998. Rehearsal in spatial working memory. *J. Exp. Psychol.: Hum. Percept. Perform.* 24 (3), 780–790. <https://doi.org/10.1037/0096-1523.24.3.780>.
- Bays, P.M., Husain, M., 2007. Spatial remapping of the visual world across saccades. *NeuroReport* 18 (12), 1207–1213. <https://doi.org/10.1097/WNR.0b013e328244e6c3>.
- Bowers, D., Heilman, K.M., 1980. Pseudoneglect: effects of hemispace on a tactile line bisection task. *Neuropsychologia* 18 (4–5), 491–498. [https://doi.org/10.1016/0028-3932\(80\)90151-7](https://doi.org/10.1016/0028-3932(80)90151-7).
- Bradshaw, J.L., Nettleton, N.C., Nathan, G., Wilson, L., 1983. Head and body space to left and right, front and rear—II. Visuotactual and kinesthetic studies and left-side underestimation. *Neuropsychologia* 21 (5), 475–486. [https://doi.org/10.1016/0028-3932\(83\)90004-0](https://doi.org/10.1016/0028-3932(83)90004-0).
- Butler, B.C., Lawrence, M., Eskes, G. a, Klein, R., 2009. Visual search patterns in neglect: comparison of peripersonal and extrapersonal space. *Neuropsychologia* 47 (3), 869–878. <https://doi.org/10.1016/j.neuropsychologia.2008.12.020>.
- Butler, S., Harvey, M., 2005. Does inversion abolish the left chimeric face processing advantage? *Cognit. Neurosci. Neuropsychol.* 16 (18), 1991–1993.
- Calen Walshe, R., Nuthmann, A., 2014. Asymmetrical control of fixation durations in scene viewing. *Vis. Res.* 100, 38–46. <https://doi.org/10.1016/j.visres.2014.03.012>.
- Chang, E., Ro, T., 2007. Maintenance of visual stability in the human posterior parietal cortex. *J. Cognit. Neurosci.* 19 (2), 266–274. <https://doi.org/10.1162/jocn.2007.19.2.266>.
- Colby, C.L., Goldberg, M.E., 1999. Space and attention in parietal cortex. *Annu. Rev. Neurosci.* 22 (1), 319–349. <https://doi.org/10.1146/annurev.neuro.22.1.319>.
- Duhamel, J., Colby, C.L., Goldberg, M.E., 1992. The updating of the representation of visual space in parietal cortex by intended eye movements. *Science* 255 (5040), 90–92.
- Heide, W., Kömpf, D., 1998. Combined deficits of saccades and visuospatial orientation after cortical lesions. *Exp. Brain Res.* 123 (1–2), 164–171. <https://doi.org/10.1007/s002210050558>.
- JASP Team, 2018. JASP (Version 0.9).
- Jewell, G., McCourt, M.E., 2000. Pseudoneglect: a review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia* 38 (1), 93–110. [https://doi.org/10.1016/S0028-3932\(99\)00045-7](https://doi.org/10.1016/S0028-3932(99)00045-7).
- Johnson, J.S., Spencer, J.P., 2016. Testing a dynamic-field account of interactions between spatial attention and spatial working memory. *Atten. Percept. Psychophys.* 78 (4), 1043–1063. <https://doi.org/10.3758/s13414-015-1058-3>.
- Kass, R.E., Raftery, A.E., 1995. Bayes factors. *J. Am. Stat. Assoc.* 90 (430), 773. <https://doi.org/10.2307/2291091>.
- Kesten, H., 1958. Accelerated stochastic approximation. *Ann. Math. Stat.* 29 (1), 41–59. <https://doi.org/10.1214/aoms/1177706705>.
- Mannan, S.K., Mort, D.J., Hodgson, T.L., Driver, J., Kennard, C., Husain, M., 2005. Revisiting previously searched locations in visual neglect: role of right parietal and frontal lesions in misjudging old locations as new. *J. Cognit. Neurosci.* 17 (2), 340–354. <https://doi.org/10.1162/0898929053124983>.
- Medendorp, W.P., Goltz, H.C., Vilis, T., Crawford, J.D., 2003. Gaze-centered updating of visual space in human parietal cortex. *J. Neurosci.* 23 (15), 6209–6214. <https://doi.org/10.1167/3.9.125>.
- Merriam, E.P., Genovese, C.R., Colby, C.L., 2003. Spatial updating in human parietal cortex. *Neuron* 39 (2), 361–373. [https://doi.org/10.1016/S0896-6273\(03\)00393-3](https://doi.org/10.1016/S0896-6273(03)00393-3).
- Mertens, I., Siegmund, H., Grüsser, O.-J., 1993. Gaze motor asymmetries in the perception of faces during a memory task. *Neuropsychologia* 31 (9), 989–998. [https://doi.org/10.1016/0028-3932\(93\)90154-R](https://doi.org/10.1016/0028-3932(93)90154-R).
- Morris, A.P., Chambers, C.D., Mattingley, J.B., 2007. Parietal stimulation destabilizes spatial updating across saccadic eye movements. *Proc. Natl. Acad. Sci.* 104 (21), 9069–9074. <https://doi.org/10.1073/pnas.0610508104>.
- Neupane, S., Guitton, D., Pack, C.C., 2016. Two distinct types of remapping in primate cortical area V4. *Nat. Commun.* 7 (1), 10402. <https://doi.org/10.1038/ncomms10402>.
- Ossandon, J.P., Onat, S., König, P., 2014. Spatial biases in viewing behavior. *J. Vis.* 14 (2). <https://doi.org/10.1167/14.2.20>. (20–20).
- Parks, N.A., Corballis, P.M., 2010. Human transsaccadic visual processing: presaccadic remapping and postsaccadic updating. *Neuropsychologia* 48 (12), 3451–3458. <https://doi.org/10.1016/j.neuropsychologia.2010.07.028>.
- Peterson, M.S., Kelly, S.P., Blumberg, E.J., 2018. Saccadic eye movements smear spatial working memory. *J. Exp. Psychol.: Hum. Percept. Perform.* <https://doi.org/10.1037/xhp0000596>.
- Pisella, L., Alahyane, N., Blangero, A., Thery, F., Blanc, S., Pelisson, D., 2011. Right-hemispheric dominance for visual remapping in humans. *Philosoph. Trans. R. Soc. London. Ser. B, Biol. Sci.* 366 (1564), 572–585. <https://doi.org/10.1098/rstb.2010.0258>.
- Pisella, L., Mattingley, J., 2004. The contribution of spatial remapping impairments to unilateral visual neglect. *Neurosci. Biobehav. Rev.* 28 (2), 181–200. <https://doi.org/10.1016/j.neubiorev.2004.03.003>.
- Posner, M.I., 1980. Orienting of attention. *Q. J. Exp. Psychol.* 32 (1), 3–25. <https://doi.org/10.1080/0033558008248231>.
- Prime, S., Vesia, M., Crawford, J.D., 2008. Transcranial magnetic stimulation over posterior parietal cortex disrupts transsaccadic memory of multiple objects. *J. Neurosci.* 28 (27), 6938–6949. <https://doi.org/10.1523/JNEUROSCI.0542-08.2008>.
- Prime, S., Vesia, M., Crawford, J.D., 2011. Cortical mechanisms for trans-saccadic memory and integration of multiple object features. *Philosoph. Trans. R. Soc. B: Biol. Sci.* 366 (1564), 540–553. <https://doi.org/10.1098/rstb.2010.0184>.
- Rabuffetti, M., Farina, E., Alberoni, M., Pellegatta, D., Appollonio, L., Affanni, P., Ferrarin, M., 2012. Spatio-temporal features of visual exploration in unilaterally brain-damaged subjects with or without neglect: results from a touchscreen test. *PLoS One* 7 (2), e31511. <https://doi.org/10.1371/journal.pone.0031511>.
- Rouder, J.N., Morey, R.D., Speckman, P.L., Province, J.M., 2012. Default Bayes factors for ANOVA designs. *J. Math. Psychol.* 56 (5), 356–374. <https://doi.org/10.1016/j.jmp.2012.08.001>.
- Russell, C., Deidda, C., Malhotra, P., Crinion, J.T., Merola, S., Husain, M., 2010. A deficit of spatial remapping in constructional apraxia after right-hemisphere stroke. *Brain* 133 (4), 1239–1251. <https://doi.org/10.1093/brain/awq052>.
- Sapir, A., Hayes, A., Henik, A., Danziger, S., Rafal, R., 2004. Parietal lobe lesions disrupt saccadic remapping of inhibitory location tagging. *J. Cognit. Neurosci.* 16 (4), 503–509. <https://doi.org/10.1162/089892904323057245>.
- SR Research Ltd., Mississauga, Ontario, Canada (n.d.).
- Ten Brink, A.F., Van der Stigchel, S., Visser-Meily, J.M.A., Nijboer, T.C.W., 2016. You never know where you are going until you know where you have been: Disorganized search after stroke. *J. Neuropsychol.* 10 (2), 256–275. <https://doi.org/10.1111/jnp.12068>.
- Umeno, M.M., Goldberg, M.E., 2001. Spatial processing in the monkey frontal eye field. II. Memory responses. *J. Neurophysiol.* 86 (5), 2344–2352. <https://doi.org/10.1152/jn.2001.86.5.2344>.
- Van der Stigchel, S., Hollingworth, A., 2018. Visuospatial working memory as a fundamental component of the eye movement system. *Curr. Dir. Psychol. Sci.* 27 (2), 136–143. <https://doi.org/10.1177/0963721417741710>.
- Van Donkelaar, P., Müri, R., 2002. Craniotopic updating of visual space across saccades in the human posterior parietal cortex. *Proc. R. Soc. B: Biol. Sci.* 269 (1492), 735–739. <https://doi.org/10.1098/rspb.2001.1935>.
- van Koningsbruggen, M.G., Gabay, S., Sapir, A., Henik, A., Rafal, R.D., 2010. Hemispheric asymmetry in the remapping and maintenance of visual saliency map: a TMS study. *J. Cognit. Neurosci.* 22 (8), 1730–1738. <https://doi.org/10.1162/jocn.2009.21356>.
- Vasquez, B., Danckert, J., 2008. Direction specific costs to spatial working memory from saccadic and spatial remapping. *Neuropsychologia* 46 (9), 2344–2354. <https://doi.org/10.1016/j.neuropsychologia.2008.03.006>.
- Vuilleumier, P., Sergent, C., Schwartz, S., Valenza, N., Girardi, M., Husain, M., Driver, J., 2007. Impaired perceptual memory of locations across gaze-shifts in patients with unilateral spatial neglect. *J. Cognit. Neurosci.* 19 (8), 1388–1406. <https://doi.org/10.1162/jocn.2007.19.8.1388>.
- Wagenmakers, E.-J., Lodewyckx, T., Kuriyal, H., Grasman, R., 2010. Bayesian hypothesis testing for psychologists: a tutorial on the Savage-Dickey method. *Cognit. Psychol.* 60 (3), 158–189. <https://doi.org/10.1016/j.cogpsych.2009.12.001>.
- Wagenmakers, E.-J., Love, J., Marsman, M., Jamil, T., Ly, A., Verhagen, J., Morey, R.D., 2018. Bayesian inference for psychology. Part II: example applications with JASP. *Psychonom. Bull. Rev.* 25 (1), 58–76. <https://doi.org/10.3758/s13423-017-1323-7>.
- Wagenmakers, E.-J., Marsman, M., Jamil, T., Ly, A., Verhagen, J., Love, J., Morey, R.D., 2018. Bayesian inference for psychology. Part I: Theoretical advantages and practical ramifications. *Psychon. Bull. Rev.* 25 (1), 35–57. <https://doi.org/10.3758/s13423-017-1343-3>.
- Wang, X., Fung, C.C.A., Guan, S., Wu, S., Goldberg, M.E., Zhang, M., 2016. Perisaccadic receptive field expansion in the lateral intraparietal area. *Neuron* 90 (2), 400–409. <https://doi.org/10.1016/j.neuron.2016.02.035>.