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Research Report

The orienting response drives pseudoneglect—Evidence from an objective pupillometric method

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ABSTRACT

Spatial attention is generally slightly biased leftward ("pseudoneglect"), a phenomenon typically assessed with paper-and-pencil tasks, limited by the requirement of explicit responses and the inability to assess on a subsecond timescale. Pseudoneglect is often stable within experiments, but differs vastly between investigations and is sometimes directed to the left, sometimes to the right. To date, no exhaustive explanation to this phenomenon has been provided. Here, we objectively assessed lateralized attention over time, exploiting the phenomenon that changes in the pupil reflect the allocation of attention in space. Pupil sizes of 41 healthy participants fixating the center were influenced stronger by the differential background luminance of the left side compared to the right side of the visual display. These differences were mainly driven by visual information in the periphery. Differences in pupil sizes positively related with greyscales scores. Time-based analyses within trials show strongest effects early on. With increasing trial number (not time), the initial leftward bias shifted central in pupillometry-based and greyscales measures. This suggests that the orienting response determines the degree of attention bias. In our amplification hypothesis we pose that the quality of pseudoneglect (i.e., the direction) is determined by higher order factors such as hemispheric imbalances, whereas the quantity (i.e., the degree) is determined by the orienting network. This account might explain numerous—previously thought opposing—findings. We here show how pupil light responses reveal pseudoneglect, in a next step, this might allow clinical diagnosis of hemispatial neglect.

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1. Introduction

Spatial attention is not diverted to sides equally, but is typically slightly biased leftward, a phenomenon termed *pseudoneglect* (Jewell & McCourt, 2000). While investigated in at least hundreds of original research works, to this day, pseudoneglect is still mostly assessed with (adaptations of) the same paper-and-pencil tasks as in the 1800s (e.g., Chodin, 1877; Fechner, 1860): marking the subjective horizontal center of a line (Jewell & McCourt, 2000). While other paper-and-pencil (e.g., greyscales; Mattingley, Bradshaw, Nettleton, & Bradshaw, 1994) and some experimental tasks (e.g., cueing, temporal order judgement; Heilman & Van Den Abell, 1979; Pérez, Pentón, & Valdés-Sosa, 2008) have been added since then, most are bound to problems such as the need to overtly respond, effects of which hand is used for responding (e.g., Jewell & McCourt, 2000), and the general inability to track how the directional bias changes on the time scale of seconds (with some exceptions, e.g., gaze position in free exploration; Chiffi et al., 2021).

1.1. Pseudoneglect

Early evidence on the capability to bisect lines converged to participants systematically overestimating one half of the line over the other (e.g., Higier, 1892). Interestingly, Wolfe (1923) reports a *rightward bias* in his systematic review, in opposition to the *leftward bias* reported in the meta-analysis by Jewell and McCourt (2000) and more recent research. Bowers and Heilman (1980) introduced the term pseudoneglect, referring to the leftward bias seen in healthy participants, as opposed to the rightward bias seen in patients with unilateral neglect after right-brain damage. An imbalance of hemispheric activity is hypothesized to be the neural underpinning of pseudoneglect, directing attention contralateral to the most activated hemisphere, with a predominant role of the right hemisphere in visuospatial processing (Benwell, Harvey, & Thut, 2014; Bultitude & Aimola Davies, 2006; de Schotten et al., 2005; Kinsbourne, 1970). The tendency toward underestimating one side relative to the other is reported to be relatively stable intra-individually (e.g., Learmonth, Gallagher, Gibson, Thut, & Harvey, 2015, 2018), but differs between individuals across age and other demographic variables such as reading habits (Chokron & Imbert, 1993; Friedrich, Hunter, & Elias, 2018; Jewell & McCourt, 2000; Learmonth & Papadatou-Pastou, 2021; Märker, Learmonth, Thut, & Harvey, 2019).

Besides the manual line bisection task, other paper-and-pencil based tasks, like the greyscales task (Mattingley et al., 2004), have shown to be sensitive to pseudoneglect. Retest-reliabilities differ between tasks and are usually better in clinical than nonclinical samples, because the latter express much weaker biases and are therefore more prone to measurement error. Despite relatively consistent biases within participants, inter-task correlations are often poor (Learmonth et al., 2015, 2018; Mitchell, Harris, Benstock, & Ales, 2020). Although perceptual tasks for pseudoneglect seem to share common mechanisms (Chen et al., 2019), stimulus properties (e.g., size, location) and other factors related to the experimental design (e.g., used hand, time-on-task, perceptual load, arousal, cueing effects) affect how strongly and in which direction a bias is expressed (e.g., Learmonth et al., 2018, 2015; Märker et al., 2019; Nicholls, Bradshaw, & Mattingley, 1999; Toba, Cavanagh, & Bartolomeo, 2011). Traditional tools for the assessment of pseudoneglect disallow tracking its course on a subsecond timescale. Altogether, there is a strong need for a more direct and potentially more detailed assessment of pseudoneglect that might help understanding what drives the direction and size of attention biases.

1.2. Pupillometry indexes the locus of covert attention

Pupil sizes not only reflect changes in brightness or accommodation, but also bodily events, changes in attention, and higher-level interpretations (Bumke, 1911; Naber et al., 2011, 2013). Recent work has revealed that the pupil actually reflects changes in differential attentional networks (alerting, orienting, executive function). Hereby, pupil size changes linked to the alerting system are mediated by a circuit centered around the locus coeruleus (LC) and the associated norepinephine system, whereas pupil size changes due to the attentional orienting response are likely mediated by a network centered around the superior colliculus (SC). Executive function, such as directed changes in focal attention, similarly affects pupil size, likely by making use of the LC or SC-centered circuits. The aforementioned changes presumably flow through the intermediate-level LC and SC centered networks (Joshi & Gold, 2020; Strauch, Wang, Einhäuser, Van derStigchel, & Naber, submitted).

Shifts in focal covert attention have been demonstrated to affect the pupil light response at constant gaze position (Binda, Pereverzeva, & Murray, 2013; Haab, 1886; Mathôt, Van der Linden, Grainger, & Vitu, 2013; Naber et al., 2013). Already in 1886, it was described how a candle, laterally positioned to fixation position in an otherwise dark room would lead to a pupillary constriction when shifting attention toward the candle, whereas shifting it back would be associated with redilation of the pupil (Haab, 1886). While this was the first description of the phenomenon, its replicability was contested (Bumke, 1911; Weiler, 1910) and ultimately forgotten until its modern (re)discovery with brightness and awareness manipulations, also for shifts in attention (Naber et al., 2011), covert attentional tracking of flickering targets (Naber et al., 2013), and covert shifts of attention to luminance-manipulated regions of the background (Binda et al., 2013; Mathôt et al., 2013). All these studies convincingly show that attending a bright or dark stimulus leads to a pupillary constriction or dilation, respectively (see Mathôt & Van der Stigchel, 2015, for a review). Covert attention to stimuli of specific brightness can therefore be decoded from pupil size.

As pseudoneglect should present itself in an automatic attentional bias toward stimuli on the left, the brightness on the left side of fixation should affect pupil size stronger than the brightness on the right side. We here use this phenomenon to reveal pseudoneglect by presenting participants with white/black hemifields or bars in the periphery while tracking the observers' pupils at constant central gaze position in two experiments.

2. Hypotheses and research questions

1. Pupil light responses predominantly reflect the brightness of the left side of the screen, given the higher prevalence of a leftward attention bias (Jewell & McCourt, 2000) (Experiment 1 and Experiment 2).
2. The pupillometry-based measure and standard pseudoneglect tasks, namely greyscales and manual line bisection tasks, are all positively linked (Experiment 2).
3. We investigated to which extent effects would be driven by the size of the black/white stimuli and their horizontal distance to the center (Experiment 2).
4. We investigated how the pupillometry-based measure and/or correlations with paper-and-pencil tasks would progress over time, providing insights into the temporal dynamics of pseudoneglect (Experiment 1 and Experiment 2).

3. Experiment 1

3.1. *Methods*

All data may be retrieved together with analysis scripts and supplementary material via the open science framework (https://osf.io/t4mq8/). The study was approved by the faculty Ethics board of Utrecht University, adhering to the declaration of Helsinki. All statistical tests reported were two-sided.

3.1.1. *Participants*

A convenience sample of fifteen participants with normal or corrected-to-normal visual acuity took part in Experiment 1 (7 = male, 8 = female, 0 = other/no preference; $M_{Age} = 25.7$, $SD_{Age} = 8.7$; all but two were right-handed). No neurological conditions were reported. Participants provided written informed consent. Handedness may affect the direction and size of pseudoneglect (Jewell & McCourt, 2000). To prevent this possible confound, analyses were conducted both on only right-handed participants and all participants (see section “Reanalysis without left-handed participants” and Supplementary Figures 7-10 in the supplementary material). Results of the right-handed participants were in line with the results of the here reported overall sample.

3.1.2. *Apparatus*

The gaze position and pupil size of the left eye were obtained with a monocular video-based Eyelink 1000 tracker (SR research) in a light and sound-attenuated laboratory. Stimuli were presented on an Asus ROG PG278Q monitor, featuring a refresh rate of 99 Hz and a screen resolution of 2560*1440 px, at 67.5 cm distance from eye-position. The participants' head was positioned in a chin and forehead rest. A standard keyboard was positioned in between the headrest and monitor. Psychopy version 2020.2.9 (Peirce et al., 2019) was used for the implementation of the experiment.

3.1.3. *Design and procedure*

First, a nine-point calibration and validation procedure of the eye-tracker was performed. The sequence of a trial is depicted in Fig. 1. To start a trial, participants had to look at a fixation cross (light grey, 18.9 cd/m^2; measured with a PhotoResearch SpectraScan PR 650 spectrometer), .34° of visual angle in both horizontal and vertical direction, presented on an intermediate grey background (6.62 cd/m^2). Once gaze position on the fixation cross within a central circle (radius of 2° of visual angle) was continuously measured for 2 sec, a trial started. During each trial, one side of the screen turned black (<.15 cd/m^2) whereas the other turned white (42.5 cd/m^2) for 5 sec, with the central circle remaining grey (6.62 cd/m^2, radius of 1° of visual angle). It was randomly determined whether the left or right side would be white or black upon trial start.

Participants were instructed to keep gaze position constant in the central circle and prevent blinking during that interval. This was their only task. After trial completion, the screen turned grey again and participants could start the next 2 sec pretrial period by pressing space bar. Trials in which participants blinked were disregarded in the analysis. The experiment ran until 10 successful complete trials were absolved per condition, resulting in a testing duration of about 4–5 min per participant.

3.1.4. *Data processing*

All data was processed using a customized Python (3.8) script. Statistics were conducted in JASP (JASP Team, 2021). The last 200 msec of the pretrial period served as baseline for the pupillary change, that is, its average was subtracted from following data points. Visual inspection shows that pupil measurements were valid with no outliers or blinks distorting the signal.

Pupil size data is given as change from the baseline, averaged across participants, in arbitrary units over time. Pupillary constrictions relative to baseline are indicated by negative values on the *y*-axis, pupillary dilations by positive values on the *y*-axis. The pupillary light response commonly overshoots (i.e., constricts a lot) for (sudden) bright stimulation. We computed the degree of this overshooting part of the light response, the constriction amplitude, by calculating the difference between baseline pupil size and the local minimum of pupil size observed within the first 2000 msec from trial onset. Differences between constriction amplitudes for black/white and white/black screens in turn indicate differences in pupil light responses between displays, besides effects of overall (similar) brightness.

3.2. *Results*

Fig. 2 depicts average pupil courses over time for the black/white and white/black screen configurations (A), as well as the functional difference between these courses (B). Pupils constricted upon trial start, a phenomenon which has previously been linked to an overall increase in luminance and visual change (Naber et al., 2013). The difference in pupil size for black/white relative to white/black was found to be statistically significant using a *t*-test for paired samples on the interval of 500–5000 msec (i.e., the end of a trial; $t(14) = 2.22$, $p = .043$). This difference in pupil size was most pronounced shortly after the initial constriction. Indeed, the constriction amplitude, calculated as the amplitude from baseline to the minimum within the first 2000 msec of trials relative to

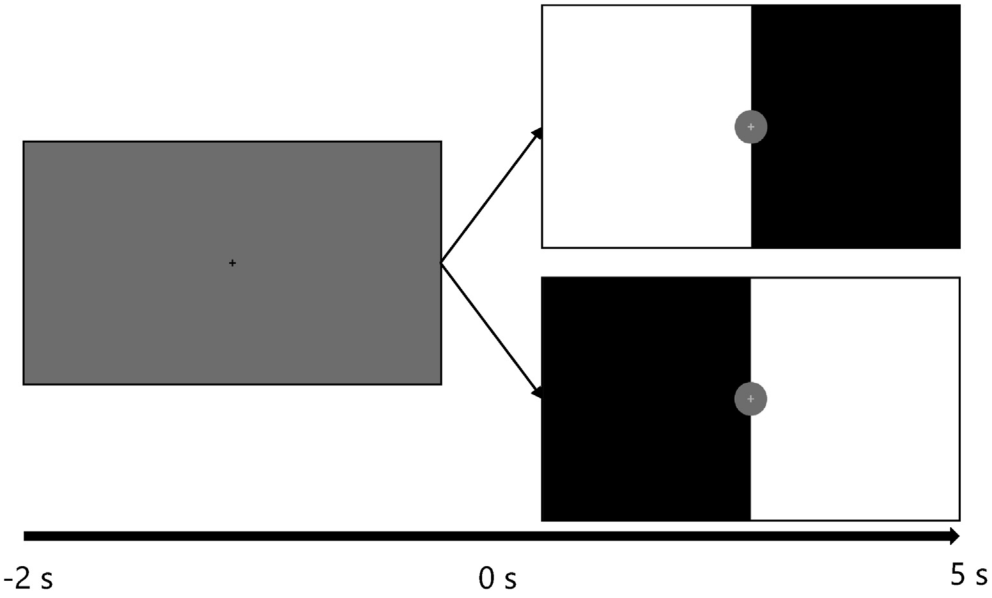

Fig. 1 – Sequence of a trial. Participants first had to keep their gaze position on a black fixation cross (within a radius of 1° of visual angle) presented on a grey background, for 2 sec. After 2 sec, the actual trial started with the left and right side turning suddenly black or white. Gaze position needed to be kept in the circle for another 5 sec to successfully absolve the trial.

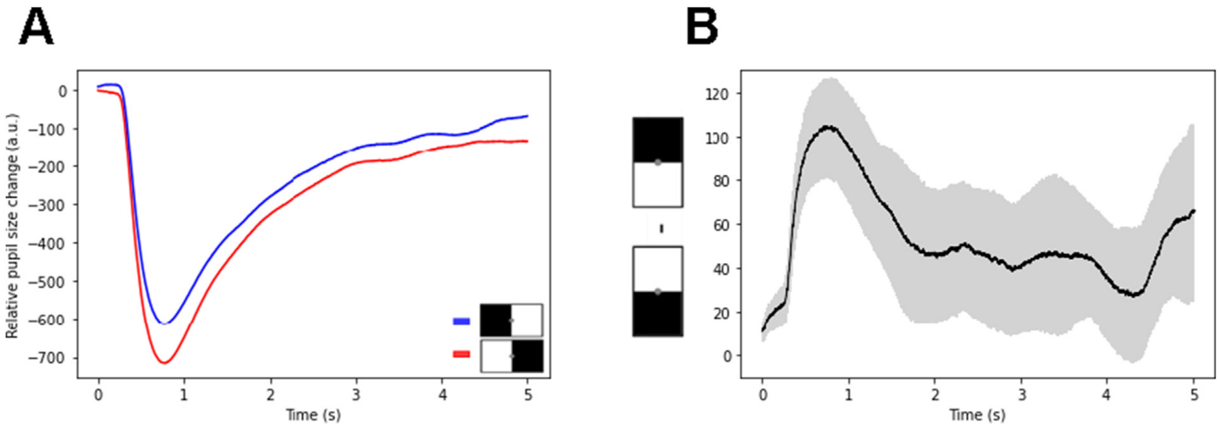

Fig. 2 – (A) Averaged pupil size changes relative to baseline over time in arbitrary units (a.u.). After the initial constriction corresponding to the increase in contrast/overall illuminance, pupils constricted less for trials during which the left side was black (blue line) and stronger for trials during which the left side was white (red line). Negative values on the y-axis indicate a smaller pupil size compared to the foregoing baseline featuring a grey screen. (B) Functional difference between averaged pupil size changes from A. Shaded grey areas represent the functional standard error of the mean. Positive values indicate a relatively larger pupil size for black/white than for white/black.

baseline pupil size, yielded a large significant difference ($t(14) = 4.73$, $p < .001$, $d = 1.22$). This indicates that spatial attention was directed toward the left side of the display. We analyzed gaze position over time to check whether slight gaze position changes to either side might have caused effects (rather than covert attentional biases). Neither horizontal nor vertical gaze position differed significantly between conditions, see Supplementary Figure 1. That said, an overall change in gaze position of about 15 px in both x- and y-coordinates (x: .363° of visual angle; y: .558° of visual angle) co-occurred with pupil size changes, which is in line with reports on pupil size systematically distorting the estimated gaze position (Drewes, Zhu, Hu, & Hu, 2014; Hooge, Hessels, & Nyström, 2019).

3.3. *Interim discussion Experiment 1*

While pupil size differences suggest pseudoneglect towards the left side of the display, this was not assessed with standard psychometric tasks as a reference. To provide this reference, both manual line bisection (Chodin, 1877) and greyscales (Mattingley et al., 2004) were assessed in Experiment 2. Furthermore, pupil size was obtained for both eyes instead of only the left eye.

To investigate whether foveal or peripheral regions drove pseudoneglect in Experiment 1, we used six conditions with white/black bars located at varying eccentricities. A control condition with horizontal bars was included, which should not lead to correlations between pupillometry-based and greyscales or manual line bisection scores.

4. Experiment 2

4.1. Methods

4.1.1. Participants

A total of 26 participants with normal or corrected-to-normal visual acuity took part in Experiment 2 ($10 = $ male, $16 = $ female, $0 = $ other/no preference, $M_{Age} = 23.6$, $SD_{Age} = 2.45$). All but four participants were right-handed. No neurological conditions were reported. Participants provided written informed consent.

4.1.2. Design and procedure

Fig. 3 visualizes a trial sequence in Experiment 2 for the pupillometric assessment. Pretrial periods were exactly as in Experiment 1, however, trials were picked from a set of 16 possible conditions in random order. Conditions included one replication of Experiment 1 (i.e., one side black, one side white), five conditions with differentially large horizontally centered grey bars (sizes degree visual angle: 3.4, 9.7, 16.4, 22.2, 28.8) between white and black areas, and two control conditions with upper and lower half of the screen being black/white with a horizontal grey bar (size degree visual angle: 5.5, 8.9). Deviating from Experiment 1, the central circle was removed from the display. Apart from the full hemifield conditions, the transitions between grey and white/black were gradual within .82 degree of visual angle. Participants needed to absolve six trials per condition with black and white sides being balanced, for both left and right eye in blocks (two blocks of $8 \times 2 \times 3 = 48$ trials, hence 96 trials in total; the sequence for blocks counterbalanced between participants). The instruction given to participants was exactly as in Experiment 1, namely to keep looking at the central cross without blinking during trials. The experiment took about 45 min to absolve, data from the left and right eye were fused.

The greyscales task and manual line bisection task were administered on a separate laptop (screen properties: 29.5 cm * 17.2 cm, 1920*1080 px). Participants were seated at 45 cm from the screen. Greyscales task stimuli were produced using MATLAB version 2019b and consisted of pairs of rectangles (“greyscales”). Each rectangle contained 50 rectangular strips of either 8, 10, or 12 px wide and 49 px high (Mattingley et al., 1994; Nicholls et al., 1999). All pixels in the first strip were white. For each subsequent strip, one black pixel per column was added at a random location up until the final strip in which there were only black pixels. This created a gradient across the width of the rectangle. The rectangle had a black outline of 1 pixel. Rectangles were re-scaled so that they had a height of .99 degrees of visual angle, and a width of either 11.43, 9.59, or 7.72 degrees of visual angle. Rectangles within a pair had the same width and were presented .99 degrees of visual angle above each other. Per pair, each rectangle displayed gradients in opposite directions. Depending on the condition, the gradients were either balanced, or biased toward bright or dark (for more information, see below). A greyscales trial started with a central fixation cross (black,

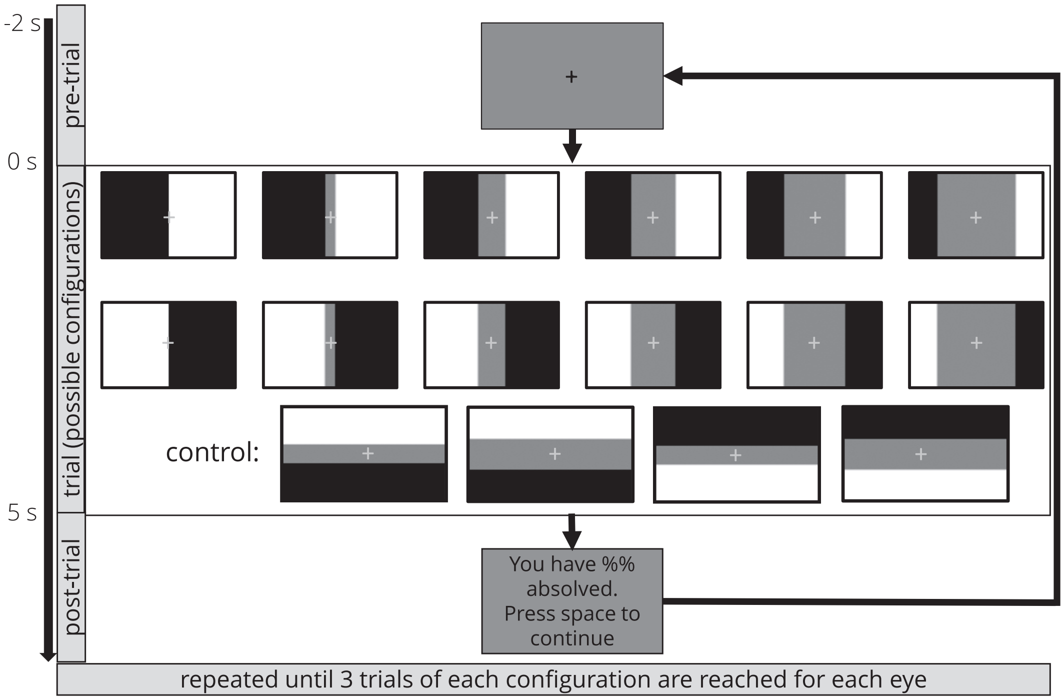

Fig. 3 – Sequence of a trial in Experiment 2; timing as in Experiment 1. Trials could feature either a vertical (experimental) or horizontal configuration (control). Trials were picked without replacement in random order until all configurations (central box) were presented three times for the tracked eye. After that, the experiment was repeated while tracking the other eye.

.28 * .28 visual degrees). After 500 msec, the greyscales stimulus was presented for 200 msec. Participants were instructed to choose which rectangle was lighter or darker by pressing the “y” key with the index finger of the right hand for the top rectangle, or the “b” key with the index finger of the left hand for the bottom rectangle. The requested target after practice (i.e., indicate lighter/darker bar) was counterbalanced between participants. A trial was terminated upon response or if no response was given after 2000 msec (5000 msec during practice). The inter-trial interval was 500 msec. Participants started with a block of six practice trials, for which one of the two rectangles was darker than the other (i.e., 75% black/25% white, *vs* 50% black/50% white). After each trial in the practice block, feedback on accuracy was provided. In the main task, all stimuli contained two rectangles that were 50% black and 50% white. Stimuli of each width and rectangle position (i.e., darker at the left end in the top, at the right end in the bottom rectangle, or vice versa) were presented 12 times, resulting in 72 trials in total. Trials in which responses were too slow were excluded.

The manual line bisection task was based on a task of McIntosh, Schindler, Birchall, and Milner (2005) and used 32 horizontal line stimuli (black), presented one by one on a white background; although shorter line lenghts were used. There were eight repetitions of four unique lines, created by connecting two left endpoint positions (−4.85° in visual angle and −2.45° in visual angle from the horizontal center of the screen) with two right endpoint positions (2.45° in visual angle and 4.85° in visual angle from the horizontal midline of the screen), resulting in three possible line lengths (4.89, 7.28, and 9.71° in visual angle). Participants were asked to indicate the subjective midpoint of each line by a click with the computer mouse. The outcome measure was the percentage deviation to the left or right from the true center (deviation score in mm/line length in mm * 100), ranging from −50% (leftward deviation) to 50% (rightward deviation). Example stimuli used in the greyscales and manual line bisection task are depicted in Fig. 4.

4.2. *Results*

Overall, pupils' constriction amplitudes were less pronounced during the black/white compared to the white/black display, despite similar brightness overall. In other words, the left half of the display affected the pupillary light response disproportionately more than the right half ($t(25) = 2.07$, $p = .049$, $d = .40$; Fig. 5). This suggests a preference of the pupil to respond to the left side of the display and replicates Experiment 1, albeit at much smaller effect size. Descriptively, all conditions showed smaller pupils when the left side of the visual display was white compared to when the left side was black (Fig. 6). As in Experiment 1, the difference in pupil response was most pronounced at the initial constriction. The difference in constriction amplitude was highly, positively correlated with the greyscales scores at $r = .51$ ($p = .011$). The retest-reliability of the greyscales task naturally limits correlations to a maximum of $r = .59$ (Learmonth et al., 2015, 2018). Hence, an attenuation correction for the presumed retest-reliability of the greyscales task was performed, suggesting an overall correlation of $r_{\text{adjusted}} = .91$. Functionally, the correlation reached a plateau after about 650 msec and remained relatively constant with a slight descriptive decrease after 2500 msec over the whole duration of stimulus presentation (Fig. 5C). In all of the six conditions (Fig. 6), but not the two control conditions (Supplementary Figure 2), a consistent descriptively positive relation between the difference in pupil constriction amplitude for screen configurations (white/black minus black/white) and greyscales scores was found.

The pupillometry-based measure did not correlate with the manual line bisection score ($r = .01$, $p = .969$; see Supplementary Figure 4 for functional correlation and (non-) significance).

In line with the literature on pupillometry (Naber et al., 2013) and paper-pencil-based assessments of pseudoneglect (Scarisbrick, Tweedy, & Kuslansky, 1987), the control conditions showed a more profound pupillary light response toward the upper half of the screen (Supplementary Figure 3; $t(25) = 8.68$, $p < .001$). As expected, no significant correlation between the greyscales scores and the difference in constriction amplitudes was found for the average of both control conditions ($r = .12$, $p = .572$). Similarly, no such correlation was observed for the manual line bisection task ($r = .20$, $p = .356$). Gaze positions in the horizontal and vertical directions were comparable between conditions and, as in Experiment 1, did not differ significantly between conditions (Supplementary Figure 2). The manual line bisection and greyscales tasks did not correlate with each other ($r = -.01$, $p = .948$).

4.3. *Interim discussion Experiment 2*

As in Experiment 1, pupil constrictions were shaped stronger by the left than the right side of the visual display, albeit at

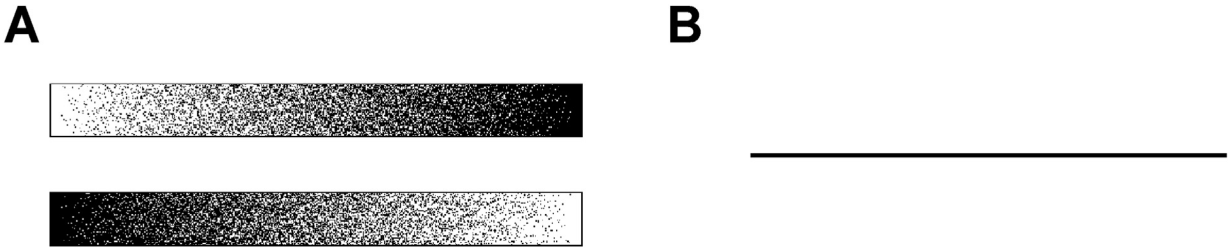

Fig. 4 – (A) Example of a stimulus used in the greyscales task. Participants need to pick the seemingly lighter/darker bar. Which bar is presented above and which below is balanced. (B) Example of a stimulus used in the manual line bisection task. Participants need to mark the horizontal center of the line.

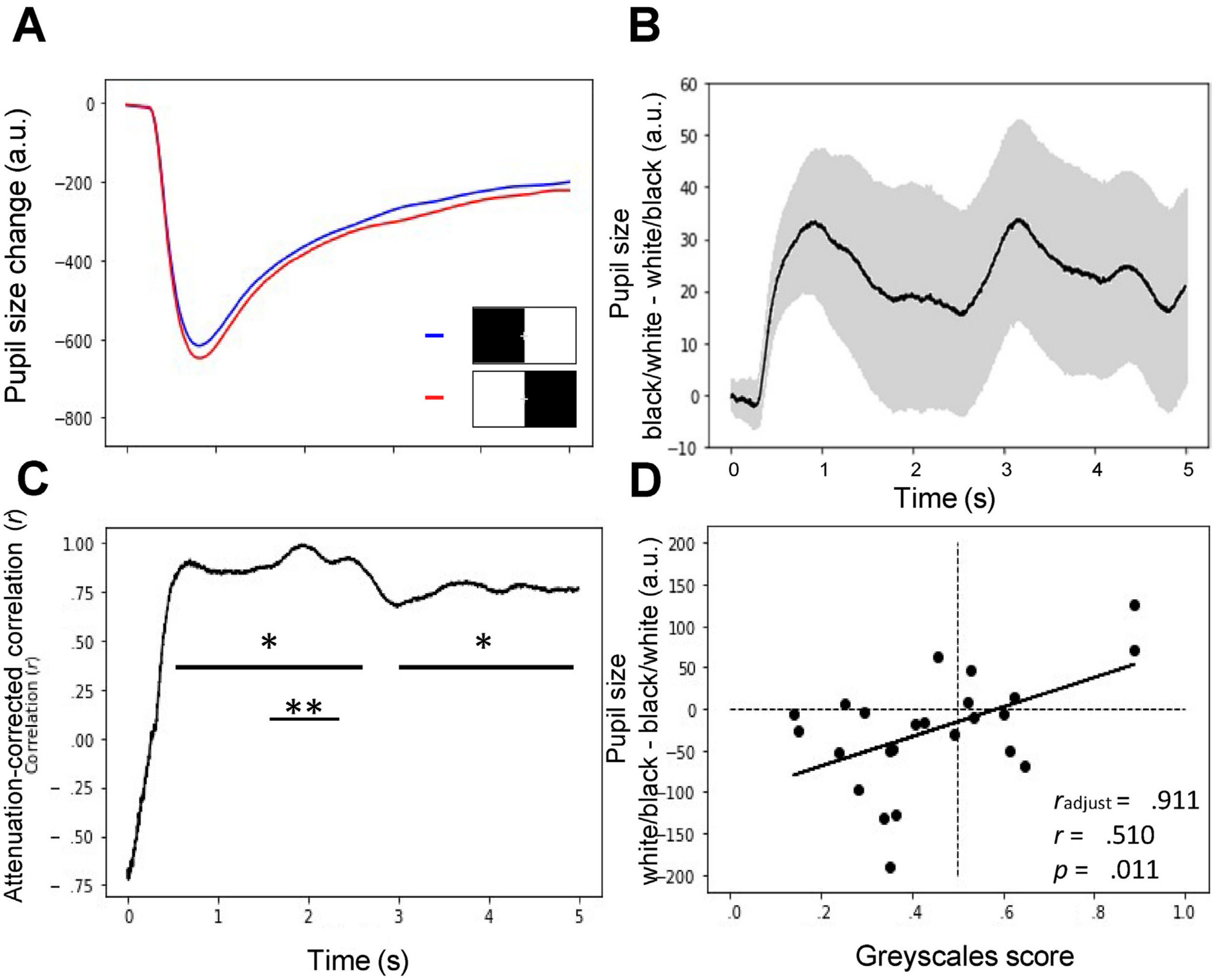

Fig. 5 – Averaged results across all but the control conditions. (A) Average pupil size in response to black/white (blue line) and white/black (red line) relative to baseline in arbitrary units (a.u.). Negative values on the y-axis indicate a smaller pupil size compared to the pretrial baseline featuring a grey screen. (B) Functional difference between averaged pupil size changes from A. Shaded grey areas represent the functional standard error of the mean. Positive values indicate a relatively larger pupil size for black/white than for white/black. (C) Attenuation-adjusted (for the retest reliability of the greyscales task) correlation between this difference and the greyscales-based measure over time. (D) Differences in constriction amplitude between white/black and black/white against greyscales score together with adjusted and unadjusted correlations. Negative values on the *y*-axis indicate a leftward bias for the pupil measure, values smaller than .5 on the *x*-axis indicate a leftward bias in the greyscales score; * = $p < .05$, ** = $p < .01$.

smaller effect size. As Experiment 2 lasted longer than Experiment 1, the leftward bias might have shifted to the right during the experiment, as reported by a study with similarly long experiments (Manly, Dobler, Dodds, & George, 2005). The difference between pupil responses was overall highly correlated to greyscales, but not manual line bisection scores, suggesting that the former two are measuring a highly overlapping construct.

4.4. *Overarching analysis*

In order to provide a better estimate of the effect size, data of Experiment 1 and Experiment 2 were fused and revealed a highly significant difference in pupil size between the screen configurations for the constriction amplitude ($t(40) = 4.78$, $p < .001$, $d = .75$); see Supplementary Figure 5 for a Bayesian sequential analysis); average pupil effects are depicted in Fig. 7A. The distribution of average pupil values indicates an overall leftward preference (Fig. 7B) which is in line with results on a left-sided bias in manual line bisection and greyscales for younger samples (e.g., Jewell & McCourt, 2000; Nicholls et al., 1999; Yamashita, 2021).

4.5. *Post-hoc analysis*

Pseudoneglect has been proposed to shift from a leftward bias to no bias with increasing time-on-task, which has been explained by an effect of reduced alerting/arousal on pseudoneglect (Manly et al., 2005). Could such effects explain the smaller pupillometry-based effects in Experiment 2 (45 min) compared

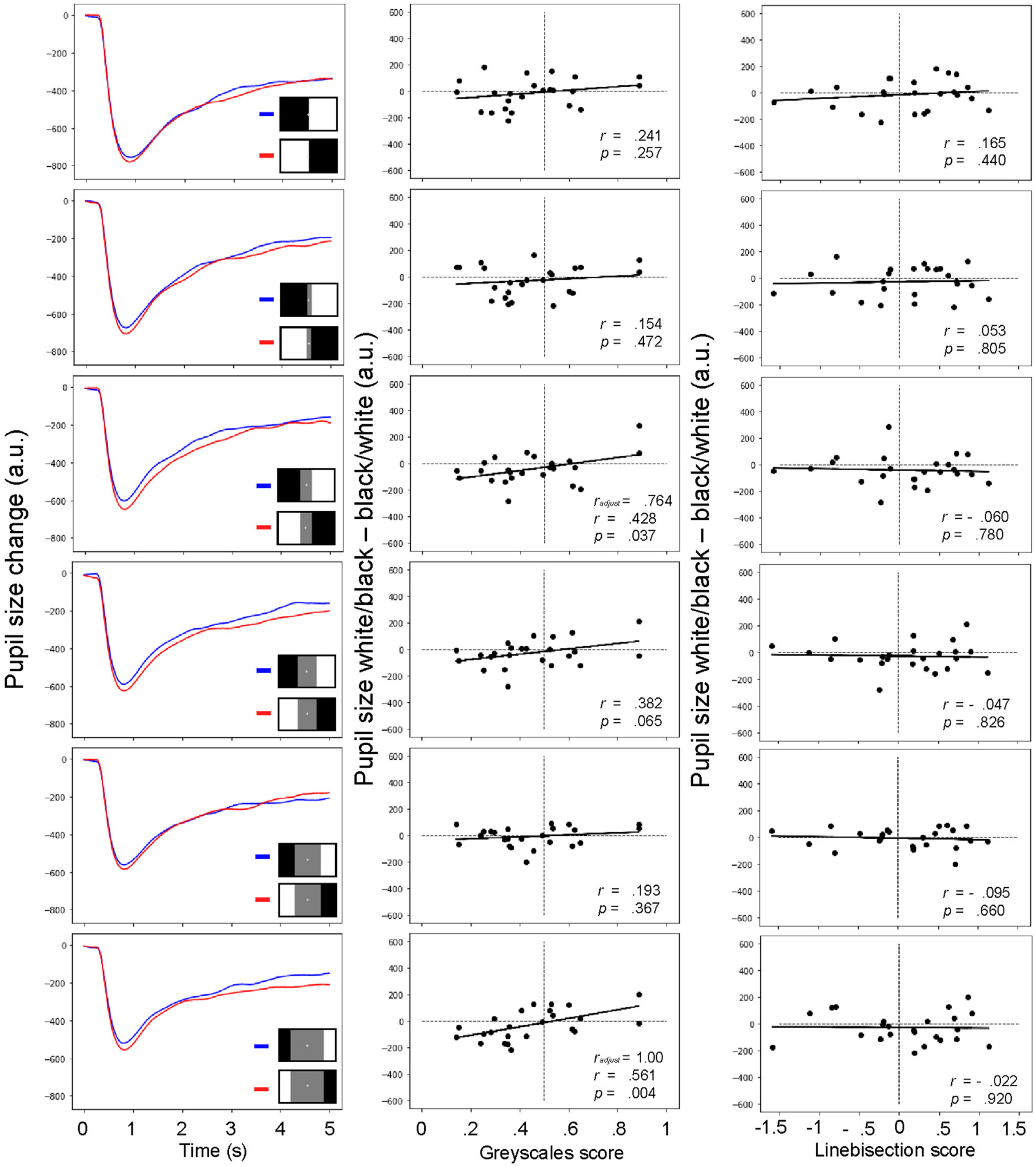

Fig. 6 – Full results of Experiment 2. Left-hand panels: Pupil response over time to black/white (blue lines) and white/black (red lines) in arbitrary units (a.u.). Central panels: Differences in pupil constriction amplitude between white/black and black/right plotted against the greyscales score. Negative values on the *y*-axis indicate a leftward bias for the pupil measure, that is, relatively stronger constriction for white/black than for black/white, values smaller than .5 on the *x*-axis indicate a leftward bias in the greyscales score. Right-hand panels: Pupil data against the line bisection score. Negative values on the *x*-axis indicate a leftward bias in the line bisection score.

to Experiment 1 (5 min)? Trials were presented in a random sequence in Experiment 2. To investigate sequence effects, sequential pairs of horizontally mirrored conditions were matched and respective difference scores were calculated. These difference scores were averaged in eight bins of 12 trials each; each bin thus contained an average of 6 difference scores.

Fig. 8 depicts the average difference in constriction (amplitude) in pupil size, split per bin. Analyzing sequence

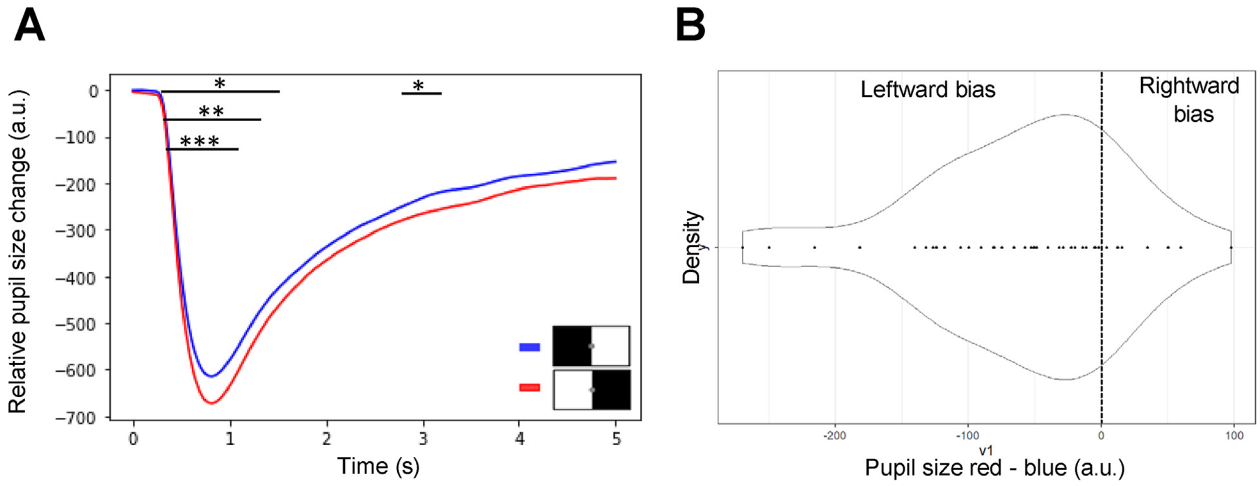

Fig. 7 – Aggregated pupil-results of Experiment 1 and Experiment 2. (A) Pupil response to black/white (blue line) and white/black (red line) in arbitrary units (a.u.). Negative values on the *y*-axis indicate a pupil constriction relative to the pretrial baseline (i.e., a grey screen). Significance levels for the difference between red and blue according to the horizontal bars; $* = p < .05$, $** = p < .01$, $*** = p < .001$. (B) Violin plot of the distribution of average difference in pupil constriction amplitude between screen configurations across participants. The vertical dotted line at $x = 0$ indicates no bias to either side as indexed by the pupil measure. Negative values indicate a bias to the left side, that is, pupils constricting more for white/black than for black/white stimuli, while positive values indicate a bias to the right side.

effects revealed a shift from a leftward bias, to no bias over bins ($F(7) = 2.49$, $p = .021$). There was a leftward bias in the first bin ($BF_{10} = 18.11$, $t(25) = 3.43$, $p = .002$). This leftward bias was also found for the second bin, but reduced in size ($BF_{10} = 4.13$, $t(23) = 2.72$, $p = .012$). With increasing experiment trial number, evidence for the absence of a bias increased ($BF_{10} = .24$ for bin 6, $BF_{10} = .23$ for bin 7, and $BF_{10} = .24$ for bin 8; all $p \geq .7$). A correlation between the number of the bin and the difference in constriction amplitude amounts to $r = -.803$, suggesting a decreasing leftward bias over bins, but should only very cautiously be interpreted, as the number of just eight data points makes significance testing superfluous. Interestingly, as opposed to the difference in constriction amplitudes, constriction amplitude itself did not change over bins ($F(7) = .65$, $p = .710$), *it was the difference alone that changed*. Together, this suggests that side differences were especially pronounced in their effect on pupil sizes in the beginning of the task. Note however, that the tracked eye changed between bin four and bin five, which might have partially but not fully contributed to this effect.

We additionally analyzed potential time-on-task effects in the greyscales and manual line bisection task. Note that these tasks were administered always after the pupil-based task and had much shorter durations (greyscales: $M = 2.09$ min, $SD = .23$ min; manual line bisection task: $M = 2.43$ min, $SD = .61$ min). The 72 trials of the greyscales task were grouped into 8 bins of each 9 trials. There was a difference in attention bias between bins ($F(7) = 2.09$, $p = .048$; see Supplementary Figure 6 for a visualization with violin plots). There was a leftward bias in the second ($BF_{10} = 1.91$, $t(23) = 2.30$, $p = .031$) and fourth bin ($BF_{10} = 1.88$, $t(23) = 2.29$, $p = .032$), and no bias in the other bins (all $p \geq .141$). There was no overall leftward or rightward bias in the greyscales task ($t(24) = 1.26$, $p = .220$). For the manual line bisection, 32 trials were grouped into eight bins of each 4 trials. There was no difference between bins ($F(7) = 1.10$, $p = .369$; see Supplementary Figure 7 for a visualization with violin plots). Crucially, in none of the bins (all $p \geq .277$), nor in the overall task $t(23) = .63$, $p = .533$), there was a leftward or rightward bias. This suggests that the manual line bisection task used in the current study was not sensitive enough to capture pseudoneglect, which could relate to the task itself and/or to the moment of task administration (i.e, the final task of the experimental session).

5. General discussion

We described a pupillometry-based method to assess pseudoneglect by exploiting the phenomenon that the pupil light response is shaped by the brightness of covertly attended stimuli and backgrounds (Binda et al., 2013; Haab, 1886; Mathôt et al., 2013; Naber et al., 2013). Our findings demonstrate that besides directed focal attention (Binda et al., 2013; Haab, 1886; Mathôt et al., 2013; Naber et al., 2013), also more automatic aspects of spatial attention can be captured by the pupil light response.

Pupils responded stronger toward luminance manipulations in the left versus right visual hemifield, which is in line with previous meta-analyses on pseudoneglect (Jewell & McCourt, 2000). Overall, the pupillometry-based measure was positively related with the greyscales task ($r = .91$ for the difference in constriction amplitude after attenuation correction). Differences in pupil size obtained from the control condition with horizontal instead of vertical bars showed no link to the greyscales task. Neither an overall correlation nor consistent pattern across conditions was observed between the pupillometry-based measure and the manual line bisection task, still, a nonsignificant correlation peak was observed

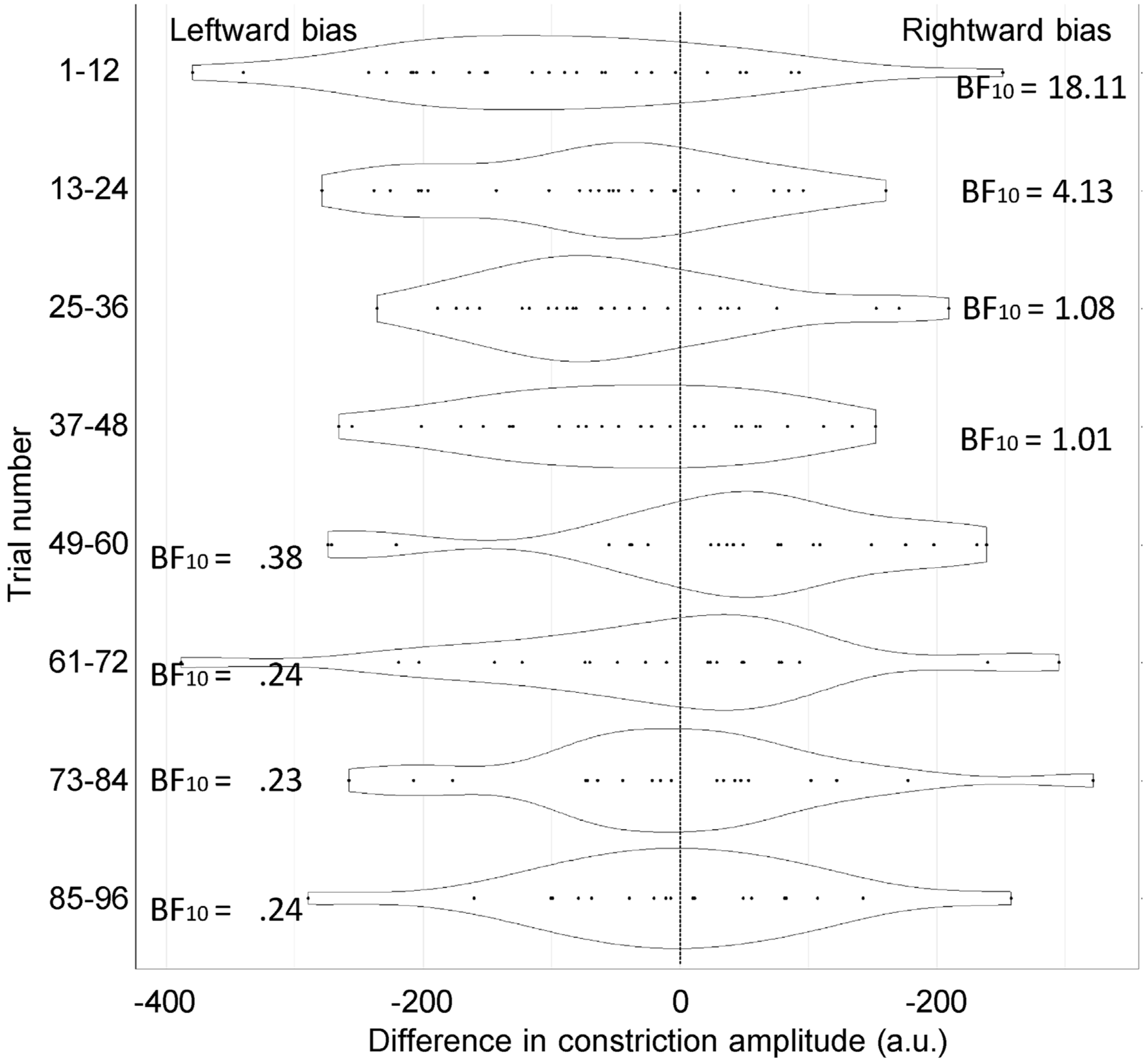

Fig. 8 – Distributions of differences in constriction amplitude between averaged side configurations grouped by trial number. Early trials (upper violin plots) show a significant bias to the left, whereas Bayes factors favor no bias for later trials (lower violin plots). Negative values indicate more constriction against the pretrial baseline for white/black than for black/white stimuli, suggesting a leftward bias.

for the same time of stimulus presentation as for the greyscales task, that is, during and shortly after the initial constriction (Supplementary Figure 4).

Previous research suggested strong sequence effects, with initial leftward bias shifting to neutral over time (Manly et al., 2005). Also here, the difference in constriction amplitude shifted from leftward to neutral over trials in Experiment 2. This explains why the difference observed between side configurations in Experiment 1 (Fig. 2B), that incorporated relatively few trials, was much stronger than in Experiment 2 (Fig. 5B). Together, time-on-task effects for the pupillometry-based measure and classical assessments strikingly overlapped, validating the here introduced method.

The size of the grey area in the center of the visual field in Experiment 2 did not affect the leftward bias negatively. Therefore, pseudoneglect appears to be driven predominantly by the representation of peripheral hemifields, rather than a slight shift of a covert-attentional spotlight from central fixation. These results support a similar hypothesis based on EEG-data obtained for line bisection, with larger effects for longer lines (Benwell et al., 2014).

The most troubling findings in research on pseudoneglect, to an extent of even questioning the entire construct, concern the poor correlations between measures that in itself provide relative stability. Here, as in the past (e.g., Learmonth et al., 2018, 2015; Luh, 1995), greyscales and manual line bisection scores were found to be completely uncorrelated, whereas the correlation between the pupillometry-based measure and greyscales score was high. A hypothesized explanation for effects to diverge are task-specific processes and strategies needed for each task, such as scanning habits or hand used (Chen et al., 2019). Biases obtained on the greyscales task, for instance, have been linked to the need for a specific perceptual judgment (Chen et al., 2019; Learmonth et al., 2015, 2018). The current results, however, showing a strong relation between greyscales and the pupillometry-based measure without performance on an explicit task for the latter, question this explanation. Another explanation for the lack of a relation between manual line bisection and greyscales performance might relate to differences in task sensitivity. In the current study, participants showed a leftward bias for some trial bins in the greyscales task but not at all for the manual line bisection task. Potentially, the manual line bisection task used in the current study was not sensitive enough to capture pseudoneglect. This could relate to the line lengths (i.e., 4.89, 7.28, and 9.71° in visual angle) which can be categorized as "short" according to Jewell and McCourt (2000), and have been (inconsistently) related to a lack of leftward bias (Jewell & McCourt, 2000).

Relying on the preserved temporal information, we suggest an alternative explanation for why measures of pseudoneglect, meant to assess the same construct, do not converge: pupillometry-based effects were most strongly pronounced shortly after stimulus onset, that is, during an initial orienting response. These early results concur with EEG-data showing pseudoneglect-related activity in an early time window (100–200 msec) (Benwell et al., 2014).

The greyscales task, similarly, was presented for only 200 msec, making it plausible to assume that it captures foremost implicit and quick attentional biases. Indeed, the correlation with the difference in initial constriction was higher than the correlation for the overall trial. The line bisection score, however, more sensitively captures later and more explicit biases as observers receive unlimited time to perceive and estimate a line's center. Different facets of pseudoneglect could thus be separated (or partially overlap) on a temporal continuum, with facets not necessarily needing to be correlated as hemifields are processed over time and/or predominantly in a bottom-up or a top-down manner. While this awaits further empirical validation, time-continuous assessment of pseudoneglect, as presented here, might hold the key to decipher the enigma that the inconsistencies within different measurements of pseudoneglect still pose.

Wolfe (1923) reports pseudoneglect to the right in his systematic review on early work into pseudoneglect, whereas Jewell and McCourt (2000) find it to the opposite direction in their meta-analysis—who is correct? Our results suggest: both are. The inconsistent findings might relate to how long experiments took, or to be more precise, how many trials there were per participant. Research reviewed by Wolfe (1923) features within-subjects designs with few participants, but often many thousands of trials each. Instead, more recent experiments, as analyzed by Jewell and McCourt (2000), are often shorter, but feature more participants. What drives this change in direction with an increasing number of trials? Alerting/arousal has been described to play a key role, with the direction of attentional bias changing from left to neutral/right over time as alertness decreases (Dodds et al., 2008; Manly et al., 2005). A related explanation is habituation of the orienting response. Sequence effects between trials observed in the current study suggest that the attention bias itself is strongest when stimulation is novel—even when it is simply black/white vertical bars—but soon wears off. Similar changes were observed in the greyscales task, assessed within just two minutes.

Further, the time-continuous pupil signal showed strongest effects that temporarily match the orienting response within trials, as did previous findings obtained with multiple different methods (see Benwell et al. (2014) for EEG, Chiffi et al. (2021) for gaze-related effects, and Gigliotta, Malkinson, Miglino, and Bartolomeo (2017) for a modeling-based account). Between trial effects can then be explained by habituation to repeatedly presented stimuli, and thus a decrease in the orienting response (e.g., Waters, McDonald, & Koresko, 1977). Habituation likely affects the two-minute greyscales task almost as much as the pupillometry-measure of pseudoneglect over 45 min. Therefore, both alerting/arousal and attentional orienting affect pseudoneglect.

These accounts alone, however, do not always suffice for explaining the direction of pseudoneglect: Benwell, Thut, Learmonth, and Harvey (2013) found mirror symmetric shifts over time in pseudoneglect direction (leftward or rightward) based on initial pseudoneglect bias (right or left) with increasing time-on-task, although this might be explained by other factors (e.g., regression to the mean) and further research into these mirror shifts is warranted.

We here pose an amplification hypothesis: Higher level factors, such as hemispheric imbalance, shape the quality (i.e., direction) of pseudoneglect. The orienting network determines the quantity (i.e., degree) of attention bias to the side that is determined by the quality. Arousal arguably affects hemispheric imbalance and the visual orienting system (Corbetta & Shulman, 2011; Van Vleet & DeGutis, 2013) via its direct input from LC to SC in the brainstem (Joshi & Gold, 2020; Strauch et al., submitted). It is thus reasonable to assume effects on quality and quantity of attention bias. Habituation, for instance, is another factor that affects the orienting system and thus the strength of pseudoneglect. Higher level factors such as emotional processing see (see Strappini, Galati, & Pecchinenda, 2021, for a review) or stress levels (Somma et al., 2021) might therefore affect pseudoneglect via two routes: the quality of pseudoneglect might be altered, possibly by altering hemispheric imbalances, whereas the quantity or degree of pseudoneglect is determined by associated changes in arousal.

Ultimately, this pupillometry-based technique could be applied and tested in the clinical diagnosis of hemispatial neglect, possibly stipulating further research into which tasks may best reflect attentional biases on which time-scale, how covert attention is affected, and to offer new approaches for the development of therapeutic tools. Specifically, we expect that a similar setup as presented here would result in pupil light responses to disproportionately reflect the brightness of the right side of the display in patients with left-sided neglect. In other words, we anticipate a weaker pupil constriction for white/black stimuli and a stronger constriction for black/white stimuli with similar overall brightness between both configurations, as the right side would be (covertly and unconsciously) attended stronger. We expect the degree of difference in pupil size between white/black and black/white stimuli to be indicative of the severity of the lateralized attention bias, which is the core deficit of neglect. Given that effect sizes were particularly high in the here presented investigation, we expect our method to be highly sensitive also in a patient population. Besides demonstrating an involvement of covert attention in hemispatial neglect, as introduced here for pseudoneglect in healthy participants, this would allow to objectively assess the lateralized attention bias in hemispatial neglect.

Author contributions

C. Strauch and A.F. Ten Brink conceptualized the studies. C. Strauch, A.F. Ten Brink, and C. Romein contributed to the study design under assistance of M. Naber and S. Van der Stigchel. Implementation and data curation were performed by C. Romein under supervision of C. Strauch. C. Romein, C. Strauch, and A.F. Ten Brink performed the data analysis and interpretation. C. Strauch and A.F. Ten Brink wrote the draft of the manuscript, C. Romein and C. Strauch performed the visualization of results, and all authors provided critical review & editing.

Conflict of interest

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. No part of the study procedures or analyses was preregistered in a time-stamped, institutional registry prior to the research being conducted.

Open practices

The study in this article earned Open Data and Open Materials badges for transparent practices. Materials and data for the study are available at https://osf.io/t4mq8/

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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2022.03.006.

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