

Trunk rotation affects temporal order judgments with direct saccades: Influence of handedness



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ABSTRACT

Manipulation of the trunk midline has been shown to improve visuospatial performance in patients with unilateral visual neglect. The goal of the present study was to disentangle motor and perceptual components of egocentric midline manipulations and to investigate the contribution of individual hand preference. Two versions of visual temporal order judgment (TOJ) tasks were tested in healthy right- and left-handed subjects while trunk rotation was varied. In the *congruent* version, subjects were required to execute a saccade to the first of two horizontal stimuli presented with different stimulus onset asynchronies (SOA). In the *incongruent* version, subjects were required to perform a vertical saccade to a pre-learned color target, thereby dissociating motor response from the perceptual stimulus location. The main findings of this study are a trunk rotation and response direction specific impact on temporal judgments in form of a prior entry bias for right hemifield stimuli during rightward trunk rotation, but only in the congruent task. This trunk rotation-induced spatial bias was most pronounced in left-handed participants but had the same sign in the right-handed group. Results suggest that egocentric midline shifts in healthy subjects induce a spatially-specific motor, but not a perceptual, bias and underline the importance of taking individual differences in functional laterality such as handedness and mode of perceptual report into account when evaluating effects of trunk rotation in either healthy subjects or neurological patients.

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1. Introduction

In daily life, we typically look at objects before reaching for them. Thus, the generation of goal-directed actions requires the integration of the location of visual objects with the current position of eye, head and trunk into a body-centered, egocentric frame of reference (Cohen and Andersen, 2002; Colby, 1998). This transformation is thought to take place within the same brain regions that are also involved in spatial attention and visuomotor planning, such as fronto-parietal and superior temporal cortices (Andersen et al., 1993; Brotchie et al., 1995; Crawford et al., 2011). The critical role of those brain areas in the transformation of visual

input into an egocentric coordinate system is underlined by the occurrence of spatial neglect after lesions involving the intraparietal sulcus and the temporo-parietal junction (Chechlacz et al., 2010; Chechlacz et al., 2013; Karnath et al., 2001). Spatial neglect, a neuropsychological syndrome that occurs mostly after lesions in the right hemisphere, is characterized by impairments in the ability to orient, perceive, and respond to stimuli in the contralesional hemifield (Chokron et al., 2007).

1.1. Effect of trunk rotation on spatial performance in neglect patients and healthy subjects

One of the core deficits of spatial neglect, the strong bias of exploratory movements towards the ipsilesional space, has been proposed to result from a lesion-induced deviation of the egocentric trunk midline towards the ipsilesional space

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(Fruhmann-Berger and Karnath, 2005; Karnath, 1997, 2015; Ventre et al., 1984). In support of this theory, neuropsychological research has demonstrated that neglect patients experience a subjective shift of their trunk midline towards the ipsilesional (i.e. right) side (Ferber and Karnath, 1999; Karnath, 1994). This subjective shift of the trunk midline in neglect patients seems to be associated with the occurrence of a rightward spatial bias, as the pattern of exploratory eye movements is shifted in respect to the *objective* trunk midline, while being symmetrical in respect to the *subjective* trunk midline (Hornak, 1992; Karnath et al., 1991). Furthermore, several studies demonstrated that manipulations of the physical or perceived trunk midline (via neck muscle or caloric-vestibular stimulation) can alleviate visual neglect symptoms (Johannsen et al., 2003; Karnath et al., 1993, 1991; Rode and Perenin, 1994; Schindler and Kerkhoff, 1997; Schindler et al., 2002). Specifically, those studies reported that either physical or illusory rotations of the trunk towards the contralesional side shortened saccade latencies towards the (mostly left) neglected hemifield (Karnath et al., 1991), re-centered exploratory eye movements, and improved visual detection performance in the absence of an overt motor response (Karnath et al., 1993).

Although trunk rotation has been consistently reported to improve spatial performance in neglect patients (see Chokron et al., 2007 for review), reports of effects for either physical or perceived trunk rotation in neurologically intact subjects are inconsistent. Karnath and co-workers observed spatially biased, neglect-like oculomotor search patterns in darkness with neck-proprioceptive and caloric vestibular stimulation in healthy subjects (Karnath et al., 1996). Two other studies reported significant effects of trunk rotation on attentional and visual detection performance in healthy subjects: Employing a version of the Posner task, Grubb and Reed reported that leftward trunk rotation increased response times for invalidly cued targets in the right hemifield; and Hasselbach-Heitzeg and Reuter-Lorenz reported shortening of response times and improved detection performance in the right visual field with physical rightward trunk rotations, but no effects with leftward rotations (Grubb and Reed, 2002; Hasselbach-Heitzeg and Reuter-Lorenz, 2002). However, several other studies employing either physical trunk or neck muscle/caloric-vestibular manipulations did not find significant effects on visual detection or attentional performance in healthy subjects (Chen and Nie-meier, 2014; Rorden et al., 2001). Thus, reported effects of trunk rotation on spatial exploration or visual attention in healthy human subjects are inconsistent, and if reported, rather modest compared to effects in patients with right hemisphere damage.

1.2. Influence of hemispheric lateralization on temporal order judgments

One sensitive tool that is often used to investigate spatial attention and oculomotor biases in neurological patients (Baylis et al., 2002; Ro et al., 2001; Woo et al., 2009) or healthy subjects (Shore et al., 2001; Stelmach and Herdman, 1991; Wada et al., 2004; Zackon et al., 1999) are temporal order judgment (TOJ) tasks. In visuospatial versions of TOJ tasks, as applied in the current study, two stimuli are presented in the left and right hemifield at various stimulus onset asynchronies (SOA) and subjects are required to report the target that has appeared first. Experiments in neurological patients demonstrated that neglect and extinction patients require a lead on the order of 200 ms to judge the contralesional stimulus as appearing simultaneously with the ipsilesional stimulus (Ro et al., 2001; Rorden et al., 1997). Specifically, a number of studies reported a prior-entry bias for visual targets in the right hemifield after right hemispheric lesions due to either stroke-induced structural (Arend et al., 2008; Baylis et al., 2002; Ro et al., 2001; Rorden et al., 1997; Sinnett et al., 2007) or TMS-

induced, 'virtual' lesions (Woo et al., 2009). These studies suggest a special role of the right hemisphere in causing a rightward spatial bias, although the influence of left and right hemispheric lesions on temporal order judgment tasks have rarely been compared directly (but see Woo et al., 2009). In addition, studies in neurologically intact subjects provide initial evidence for an influence of *functional* laterality (sometimes regarded as behavioral manifestations of cerebral asymmetry) on TOJ bias, as rightward spatial biases are more pronounced in right- as compared to left-handed subjects (Efron, 1963; Geffen et al., 2000).

1.3. Goals and hypotheses of the current study

The first aim of the present study was to investigate the effect of physical trunk rotation on temporal order judgments as a function of individual differences in functional laterality. To this end, we employed visual temporal order judgment tasks with differing trunk rotations, and tested the influence of individual hand preference and ocular dominance. The second aim of the study was to discriminate between trunk-rotation induced motor biases and perceptual effects. We therefore employed two different versions of the TOJ task: In the first, congruent "motor" version, subjects were required to perform a direct saccade towards the target that had appeared first. In the second, "perceptual" version, subjects indicated the appearance of the first stimulus by performing a saccade towards an incongruent (upper or lower) screen location.

1. We hypothesized that right-handed subjects would exhibit spatially biased TOJ towards the right hemifield (i.e. prior entry bias for right targets) in the straight trunk condition, that would be amplified by rightward trunk rotation. We expected left-handed participants to show a smaller bias or the reversed pattern in the straight trunk condition, and possibly a left hemifield bias with leftward trunk rotation. These predictions were based on the consideration that trunk rotation towards the preferred hand brings the upper body and the respective dominant hand closer to the visual target, placing it in the preferred working space of the subject, and possibly increasing its behavioral relevance. Smaller spatial bias in left-handed subjects was expected based on the fact that they use both hands more flexibly in daily life. Predictions for the trunk rotation direction that does not match the dominant hand were harder to derive, but following the reasoning described above, we expected no change of TOJ bias for leftward rotations in right-handed subjects and a modest bias towards the right hemifield with rightward trunk rotation in the left-handed subjects.
2. We hypothesized that perceptual facilitation of visual stimuli toward the side of trunk rotation would be apparent in both, the spatially congruent and incongruent, task versions. In contrast, a primary effect of trunk rotation on saccade planning and/or execution would be expressed as an effect in the congruent saccade version only.

2. Methods

2.1. Participants

Forty-six volunteers without neurological illness and normal or corrected to normal visual acuity participated in our study. Six subjects (3 right-handed (RH) and 3 left-handed, (LH)) were excluded from further analysis due to poor performance (less than 75% accuracy on trials with the maximum SOA 283 ms, see below). Thus, we report data from 20 RH and 20 LH subjects for the main

Table 1
Hand and eye dominance of participants.

Handedness	N	Female N	Median age (years)	Age range (years)	Ocular dominance (right/left)
Right-handed	20	12	24.5	20–30	17 R/3 L
Left-handed	20	9	23	19–36	8 R/12 L

experiment (see Table 1). Both handedness groups did not differ significantly with respect to gender distribution (Chi-square test: χ^2 (df=1)=0.9, $p=0.34$). Ten RH and ten LH subjects additionally participated in the control experiment with incongruent saccade responses. Subjects were paid for their participation and earned an additional bonus according to their performance on trials with maximum SOA.

All subjects gave written informed consent to participate in the experiments. The study was approved by the local Ethics Committee of the Georg-August-University Göttingen according to the Declaration of Helsinki.

2.2. Assessment of handedness and ocular dominance

2.2.1. Dominant hand

Individual handedness was assessed with the Edinburgh Inventory (Oldfield, 1971). Based on the evaluation of everyday hand use, the Edinburgh laterality quotient (LQ) was computed, ranging between -100 (maximum left-hand dominance) and 100 (maximum right-hand dominance). Subjects were rated as left-handed with a $LQ < 0$ and right-handed with a $LQ > 0$ (Oldfield, 1971). Following convention, and in order to account for the skewed distributions of LQs in right- and left-handed subjects, we also calculated LQ deciles as described in Oldfield (1971) and performed additional analysis on the deciles. Right-handed subjects had a median LQ score of 91.7 (LQ range [50 100], median decile R.8, decile range [R.2 R.10]). Left-handed participants had a median LQ score of -70.8 (LQ range [$-100 -17$], median decile L.5, decile range [L.1 L.10]).

2.2.2. Dominant eye

Ocular dominance was determined using a variation of the Porta test (Li et al., 2010). Subjects were asked to hold a pen vertically with both hands and extended arms and to align the pen with a distant corner of the room (4 m away). Participants were then asked to close one eye after the other and report which eye closure led to the largest pen-corner misalignment. That eye was assumed to be the dominant eye (Table 1).

2.3. Experimental set-up

Stimuli were generated using the Presentation[®] software (Neurobehavioral System Inc., version 16.2, www.neurobs.com) and were presented on a 27 in. LCD monitor with an eye-to-screen distance of 57 cm. The screen resolution was 2560×1440 pixels. The monitor had a vertical refresh rate of 60 Hz. Real-time eye tracking was performed with a ViewPoint eye tracker (Arrington Research) running on a separate PC. Gaze position was sampled continuously with a temporal resolution of 60 Hz with a mini-IR sensitive camera placed below subjects' right eye, transferred to the Presentation PC using the ViewPointClient Ethernet Interface and recorded together with stimulus and timing information. Before each experimental run the eye tracker was calibrated using a 4×5 calibration matrix.

Participants were sitting in a darkened room on a chair that was aligned to the center of the monitor. Depending on the experimental condition, the chair (and accordingly the trunk) was

oriented straight, rotated 60° to the left, or 60° to the right around the trunk vertical axis. In all trunk rotation conditions, head and eyes were facing straight ahead (Fig. 1A). The head was stabilized by a chin rest and locked tight into the position with bars pressing against both sides of the head (HeadLock[™] Ultra Precision Head Positioner[™], Arrington Research) and an additional rubber strap. The experimenter ensured that the subject's shoulder axis was parallel to the back of the seat and that the hands were positioned in line with the trunk midline. One run with a given trunk rotation lasted about 8 min, after which the subject took a break and the head was unlocked. After the break, the subject was re-positioned and the eye movements were re-calibrated. The order of trunk rotations was pseudorandomized and each rotation was tested twice within a given session.

2.4. Experimental tasks

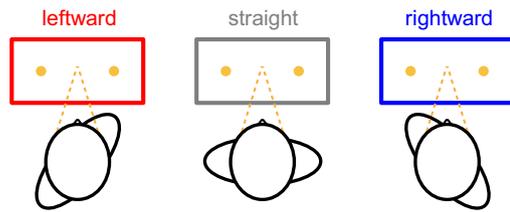
2.4.1. Main experiment (spatially congruent saccade)

Participants performed a visual temporal order judgment (TOJ) task (Fig. 1B). Each trial started with the presentation of a central fixation cross. Once subjects had acquired proper fixation for 400 ms within a 5° radius, the first peripheral target was presented in the left or in the right hemifield and the fixation cross was turned off simultaneously. After a randomized stimulus onset asynchrony (SOA) of $-283, -83, -50, 0, +50, +83$ and $+283$ ms (negative values indicating that the target in the left hemifield appeared first), the second target was presented in the opposite hemifield. Targets were presented at eccentricities of 20° on the horizontal meridian and were white filled squares with a side length of 0.5° visual angle. Subjects were instructed to perform a saccade to the target that had appeared first, as fast and as correctly as possible. They were informed to receive a bonus according to the proportion of correct and timely saccades. Targets remained on screen until one of the targets (not necessarily the first) was fixated for 200 ms within a 10° radius around the target, for a maximum of 800 ms target acquisition time. At the end of each run, the performance feedback and earned bonus were shown, based on the proportion of validly and correctly performed trials with an SOA of 283 ms (even though subjects believed that it was feedback across all SOAs). Subjects completed 2 runs with each of the three trunk rotations. Each run contained 210 trials and lasted about 8 min. Including the practice trials and the handedness/ocular dominance assessments, one session lasted about 1.5 h.

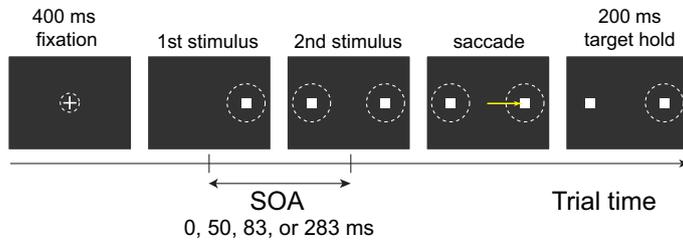
2.4.2. Control experiment (spatially incongruent saccade)

The task design was identical to the main experiment, except for the direction of saccade response. Instead of requiring a saccade directly towards the target, subjects chose one of two corresponding targets on the vertical meridian 10° above or below the screen center (Fig. 1C). The response targets were color-coded: a red dot represented the left stimulus being first and a blue dot the right target being first (subjects were trained on color-response association prior to collecting data). Response targets appeared at the same time as the first stimulus. The positions of response targets were pseudo-randomized between experimental runs to factor out possible saccade preference for the upper or lower hemifield. As in the main experiment, each trial started with the presentation of a central fixation cross. After proper fixation for 400 ms, two targets appeared at 20° horizontal eccentricity right and left of the screen. A response was counted valid when subjects fixated one of the two corresponding saccade targets for 200 ms within a radius of 5° and 1000 ms maximal response time.

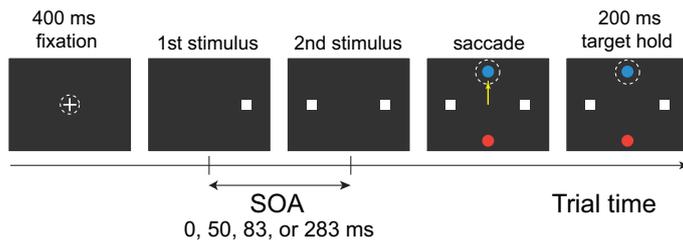
A Experimental conditions: trunk rotation



B Main experiment: congruent saccade response



C Control experiment: incongruent saccade response



D Experimental predictions and analysis measures

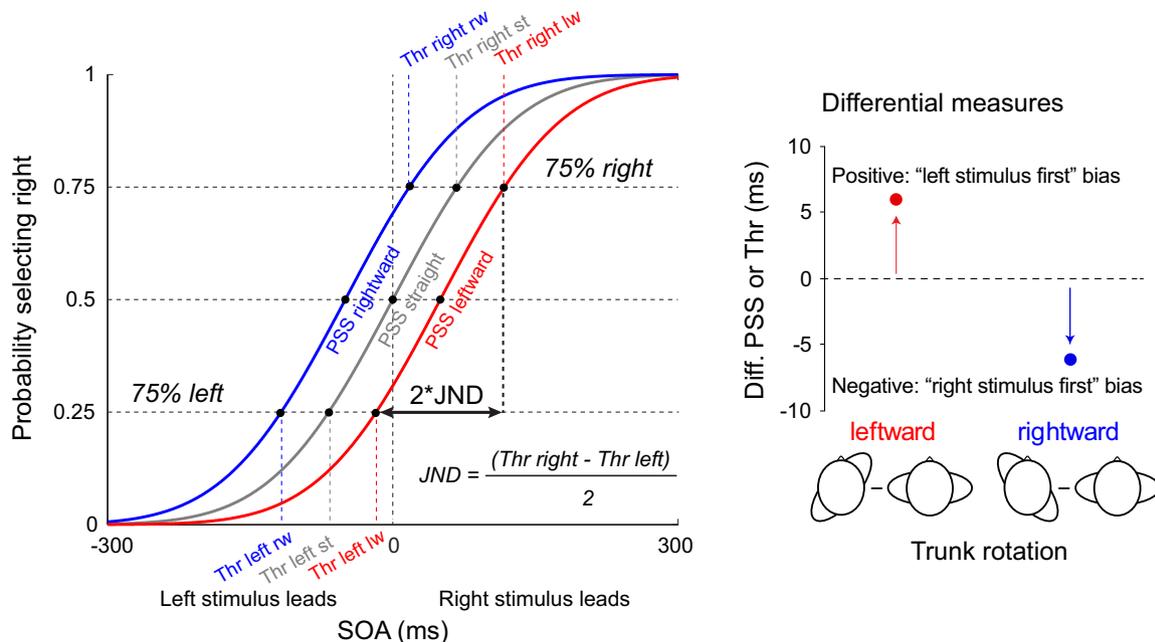


Fig. 1. Task design and experimental predictions. (A) The experiment was performed in three trunk rotations: 60° leftward, 60° rightward, and straight (baseline condition). (B) Temporal order judgment task (TOJ), congruent condition (main experiment). Trials started with a central fixation. After proper fixation two stimuli appeared with a temporal delay of 0/50/83/283 ms. Subjects were asked to saccade to the stimulus that had appeared first as fast and correctly as possible. (C) TOJ task, incongruent condition (control experiment). Subjects were asked to saccade to the color target at an upper or lower screen position according to a pre-trained rule: blue-right stimulus first, red-left stimulus first. (D) *Left panel:* idealized psychometric functions for each rotation condition and key parameters estimated from the psychometric functions of each individual subject. The *point of subjective simultaneity* (PSS) reflects the SOA by which one stimulus has to precede (or follow) the other in order for the two stimuli to be judged as simultaneous. Similarly, the *75% threshold* (Thr) reflects the SOA at which the left or right stimulus is reported as leading with 0.75 probability. For each trunk rotation condition, we calculated the threshold for 75% choice right and for 75% choice left. The *just noticeable difference* (JND) reflects the temporal sensitivity and is equal to half the difference between 75% right and 75% left thresholds. *Right panel:* differential measures (rotation condition minus straight condition). A negative differential PSS or Thr signifies a bias to report the right stimulus as leading and corresponds to a shift of the psychometric curve to the left (blue curve, rightward rotation). Conversely, a positive differential signifies a "left stimulus first" bias (shift of the psychometric curve to the right, red curve, leftward rotation). Note that these idealized predictions assume no change in JND; a change in JND would require a change in the slope of the psychometric function. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.5. Analysis

Choice behavior was analyzed by means of psychometric modeling. We estimated the psychometric function for each participant and trunk rotation separately. To this end, a logistic function $f(x) = \gamma + (1 - \gamma - \lambda) p(x)$, where $p(x) = 1 / (1 + 10^{-\beta(x - \alpha)})$, was fitted to the choice data (probability of selecting the right target as a function of SOA, R, <https://stat.ethz.ch>, psyphy package, <https://stat.ethz.ch/R-manual/R-patched/library>, version 0.1–9, (Klein, 2001; Wichmann and Hill, 2001), function parameters: γ -lower asymptote value, λ -upper asymptote value, α -point of inflection, β -maximum slope). Model accuracy was assessed by means of goodness-of-fit coefficients (pseudo R^2) for individual subjects of both handedness groups. Three key parameters were estimated from the psychometric functions of each subject (Spence and Parise, 2010) (Fig. 1D):

1. The *point of subjective simultaneity* (PSS) reflects the time interval by which one stimulus has to precede (or follow) the other in order for the two stimuli to be perceived as simultaneous. The objective point of simultaneity in the TOJ task is at SOA 0 ms (i.e. left and right stimulus appear simultaneously). A non-zero PSS indicates that one of the two stimuli has to lead in time in order to be chosen equally often. Probability of right choice was plotted as a function of SOA. A leftward shift of the psychometric function with a resulting negative PSS indicates a bias toward “right first” reports. Conversely, a positive PSS indicates a bias toward “left first” responses, as the right target has to precede the left target to be judged as simultaneous (see Fig. 1D for experimental predictions).
2. *Thresholds* were estimated separately for left and right choices. For each trunk rotation condition, we estimated the SOA for 75% choice left and for 75% choice right.
3. The *just noticeable difference* (JND) represents the minimum SOA difference at which a stimulus can be reliably discriminated as being first and provides a measure for the temporal resolution. One half of the difference between SOA values corresponding to 75% right threshold and 75% left threshold was taken as the JND (Fischer and Whitney, 2014; Kwon et al., 2014). While JND is related to thresholds, it is a differential measure. Thus, asymmetric shifts of “left first” and “right first” branches of choice function might be more apparent in separate threshold estimates if the difference between left and right thresholds remains the same (e.g. when the entire function just shifts along the SOA axis).

Unless otherwise noted, statistical analysis was performed on PSS, Thresholds and JNDs across the individual data by a one-way repeated-measures analysis of variance (rANOVA) with the within subject factor “trunk rotation” (leftward 60°, straight 0°, rightward 60°). When appropriate, a Greenhouse-Geisser correction of the degrees of freedom was applied. Significant main effects and interactions were followed up by pairwise, Bonferroni-corrected comparisons.

2.5.1. Influence of handedness

Following the observation that handedness is not a dichotomous variable (Knecht et al., 2000; Wada et al., 2004), effects of hand preference were assessed by correlating the laterality quotient deciles obtained from the Edinburgh inventory (Oldfield, 1971) and the trunk rotation-specific PSS. We used Spearman correlation to avoid relying on the normality of deciles' distributions. To examine whether measured correlation coefficients were significant, we used a bootstrapping approach (Efron, 2011) to estimate the 95% confidence interval bounds. To this end, we randomly resampled values from the original set of 20 subjects,

1000 times, with replacement.

2.5.2. Influence of ocular dominance

Since the large majority of right-handed subjects exhibited right-eye dominance (17 of 20 subjects), the group size was too small to assess effects of ocular dominance in this group. The left handed subjects however, contained enough left-eye ($n=12$) and right-eye dominant ($n=8$) subjects to test the influence of ocular dominance (Table 1). PSS, JND and Thresholds were submitted to a mixed ANOVA with the within subject factor “trunk rotation” (leftward 60°, centered 0°, rightward 60°) and ocular dominance (left vs. right) as the between-subject factor.

3. Results

Our main experiment aimed to investigate how physical trunk rotation affects temporal order judgments (TOJ) and whether individual differences in functional laterality measures such as handedness and ocular dominance modulate these effects. For most of the results, we present data separately for right- and left-handed groups, and directly compare them at a later part of the results section. The reason for the initial separation of the two handedness groups was to ensure comparability with previous studies on trunk rotation effects, since most studies in neglect patients as well as in healthy controls included predominantly right-handed subjects. The main experiment was conducted with spatially congruent saccade choices (i.e. target and saccade report location coincided). The control experiment investigated the TOJ task with incongruent saccade locations.

3.1. TOJ performance in the straight trunk position: effect of handedness and ocular dominance

We first characterized TOJ performance in the trunk straight condition. To this end, we calculated the proportion of right-first choices as a function of SOA and determined the *point of subjective simultaneity* (PSS), *thresholds* and the *just noticeable difference* (JND) for individual right ($N=20$) and left-handed ($N=20$) subjects (see Section 2, Fig. 1D). In line with previous studies, the PSS in the right-handed group was somewhat shifted towards negative values (Fig. 2A) (Corballis, 1996; Nicholls, 1994), albeit this effect did not reach statistical significance (mean -16 ms, S.D. 39 ms, one-sample t -test: $t(19) = -1.84$, $p=0.08$). However, when we excluded one right-handed subject that exhibited an LQ of 50 only, that would be classified not as ‘right-handed’ but as ‘marginally lateralized’ in other studies, (Wada et al., 2004) the PSS shift in the right-handed group did reach significance ($t(18) = -2.2$, $p < 0.05$). This indicates a prior entry bias for right targets in right handed subjects, since stimuli in the left hemifield had to precede stimuli in the right hemifield to be reported as simultaneous.

The distribution of PSS values in the left-handed subjects was more symmetrical around zero (mean PSS -5 ms, S.D. 31 ms, one-sample t -test: $t(19) = -0.78$, $p=0.44$) (Fig. 2A). However, when right- and left-handed groups were compared directly, we did not find a significant difference in PSS ($t(38) = 0.9$, $p=0.35$). Likewise, thresholds for 75% choice right and for 75% choice left did not differ between handedness groups (all $p > 0.1$).

The temporal resolution as assessed with the JND did not significantly differ between the right- and left-handed groups (mean 86 ms (S.D. 47 ms) and mean 94 ms (S.D. 52 ms), respectively, $t(38) = 0.54$, $p=0.59$).

Apart from handedness, another measure of functional laterality in humans is the ocular dominance. In agreement with previous studies (Bourassa et al., 1996), the left-handed group contained both, left-eye dominant ($n=12$) and right-eye dominant

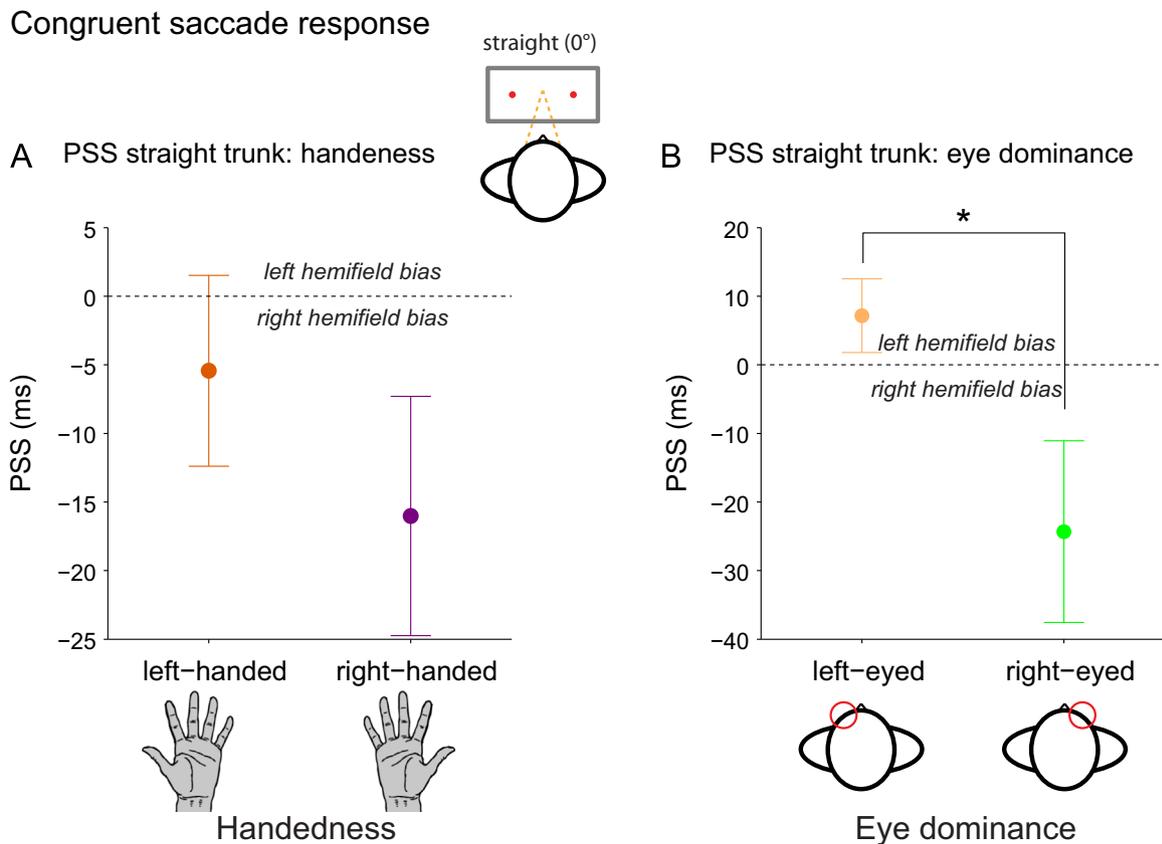


Fig. 2. Influence of handedness and ocular dominance on PSS – straight trunk. (A) Mean PSS in the straight rotation condition for right- and left-handed subjects. (B) PSS separated for left-eye and right-eye dominant left-handed subjects. Note that in our convention, a negative PSS corresponds to a “right hemifield bias”–the left stimulus has to lead in order to be perceived as simultaneous to the right stimulus. Error bars denote S.E.M. across subjects, star denotes significance at $p < 0.05$ for the specific comparison as indicated by the connecting lines.

($n=8$) subjects, while right-handed subjects exhibited mostly right-eye dominance (17 of 20 subjects). Due to the small group size of right handed subjects with left eye dominance, we could analyze only effects of ocular dominance on TOJ in the left-handed group. The PSS in the straight ahead condition differed significantly between the groups with right- and left eye dominance ($t(18)=2.5$, $p < 0.05$). This effect of ocular dominance can be attributed to the fact that right-eye dominant subjects showed a negative PSS (mean -24 ms, S.D. 37 ms) indicating a prior entry bias for right targets, while left-eye dominant subjects had a positive PSS (mean 7 ms, S.D. 19 ms) (Fig. 2B). Right- and left-eye dominant subjects did not differ in respect to their JND ($t(18)=0.19$, $p < 0.86$) or their thresholds for 75% choice right and for 75% choice left (all $p > 0.1$).

Taken together, these results indicate that ocular dominance is linked to a shift of the point of subjective simultaneity towards the dominant eye. Handedness, which is strongly confounded by ocular dominance, modulates, but does not fully account for TOJ bias in the straight trunk condition.

3.2. Influence of trunk rotation

Since the inter-subject variability in the straight-ahead condition was substantial, and since we were specifically interested in the effects of trunk rotation, we subtracted the individual PSS in the straight condition from the PSS in the leftward and rightward trunk rotation conditions, to estimate leftward and rightward differential PSS, 75% thresholds, and JND. Differential measures are plotted in the figures below for illustration purposes and non-

Table 2

Mean values and S.E.M. in ms for the main experiment with congruent saccade responses.

Congruent saccade task	Trunk rotation		
	Leftward	Straight	Rightward
Right-handed subjects			
PSS	-15 (9)	-16 (9)	-20 (9)
Threshold 75% (left choices)	-98 (14)	-100 (13)	-96 (12)
Threshold 75% (right choices)	69 (12)	71 (13)	53 (11)
JND	84 (10)	86 (10)	74 (7)
Left-handed subjects			
PSS	-1 (7)	-5 (7)	-17 (7)
Threshold 75% (left choices)	-98 (14)	-95 (11)	-118 (16)
Threshold 75% (right choices)	85 (15)	93 (17)	73 (14)
JND	92 (11)	94 (12)	95 (12)

differential mean values for all trunk rotations are provided in Table 2. The statistical analyses were performed on the original (non-differential) data from the 3 different rotation conditions.

3.2.1. Right-handed group

Fig. 3A illustrates the psychometric curves for right-handed subjects that were fitted to the mean right choice probability across these subjects, separated by trunk rotation. Trunk rotation did not lead to noticeable changes in the PSS, as can be also seen in Fig. 3B, which plots the mean difference between individual PSS in the straight-ahead condition and the two trunk rotation

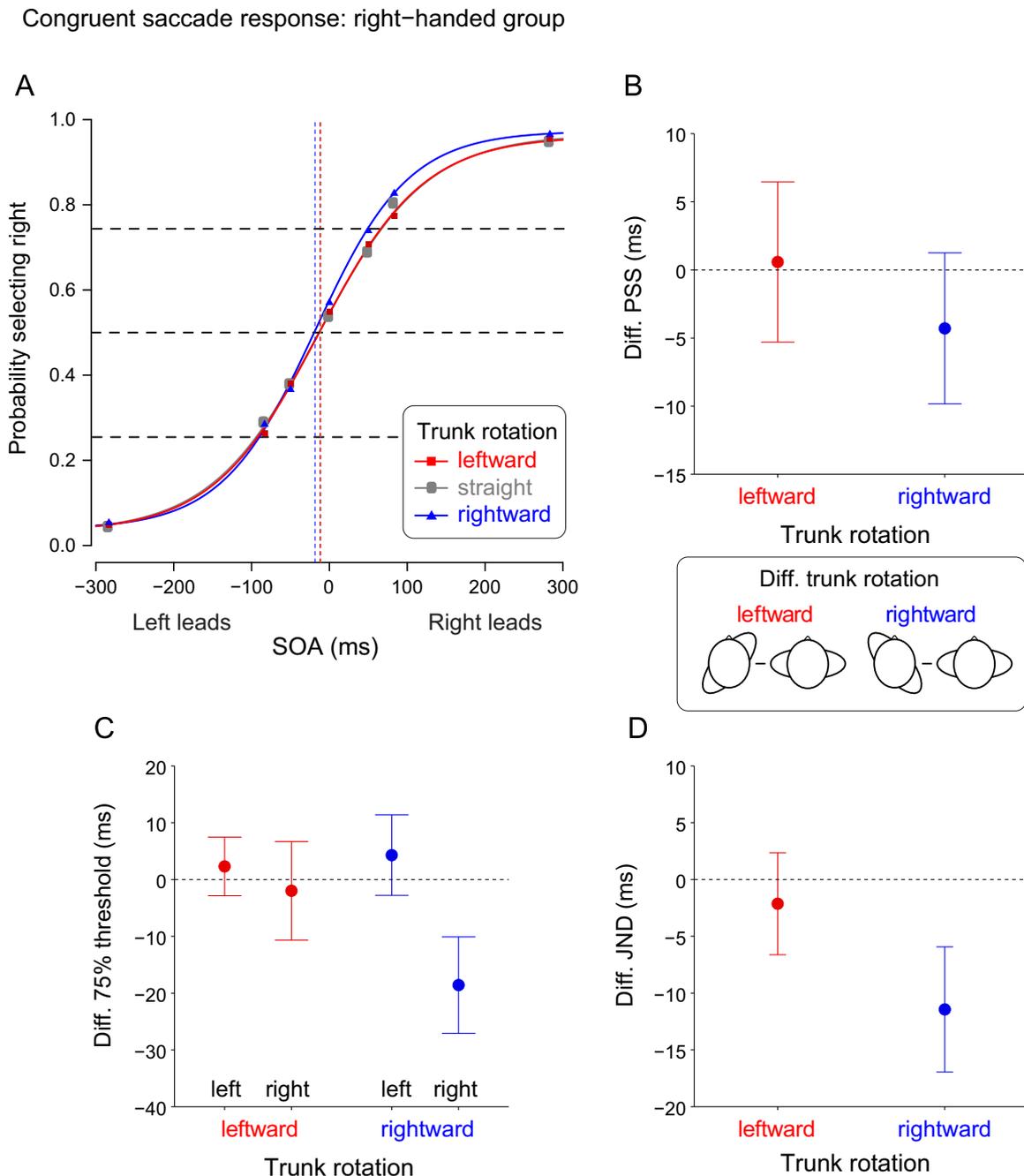


Fig. 3. Effect of trunk rotation on TOJ parameters in right-handed subjects. (A) Psychometric functions fitted to the subjects mean response probabilities for each trunk rotation condition. On the x-axis, the stimulus onset asynchrony (SOA) is marked with negative SOAs indicating left-leading stimuli. The y-axis represents the probability of right choices. The blue curve represents the rightward trunk rotation, the red curve-leftward trunk rotation, and the gray curve (mostly covered by the red curve)-the straight trunk rotation. The points of subjective simultaneity (PSS) are marked by vertical dotted lines. Horizontal dotted lines signify 25%, 50%, and 75% right choice probability, corresponding to 75% left threshold, PSS, and 75% right threshold. (B) Differential PSS ($PSS_{\text{leftward}} - PSS_{\text{straight}}$ and $PSS_{\text{rightward}} - PSS_{\text{straight}}$), for leftward and rightward trunk rotation. (C) Differential 75% left and 75% right thresholds. (D) Differential JND. On all plots in B, C and D, means and S.E.M. across subjects are shown. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

conditions. Accordingly, the rANOVA with the factor trunk rotation (leftward, straight, rightward) revealed no main effect of trunk rotation on PSS ($F(2,38)=0.41$, $p=0.66$), confirming that trunk rotation did not result in a shift of PSS towards either hemifield. Inspection of the psychometric fits suggested that rightward rotation was associated with a shift towards smaller SOA at 75% right choices in the rightward rotation condition, and thus in an increased probability of right targets being reported as leading (cf. Fig. 3A, blue curve). To confirm this, we analyzed trunk rotation effects on thresholds for 75% left and right choices separately. This

analysis revealed that trunk rotation significantly affected thresholds for right choices ($F(2,38)=3.3$, $p < 0.05$), while not affecting thresholds for left choices ($F(2,38)=0.198$, $p=0.82$). Fig. 3C shows that this effect was indeed due to the decrease of 75% right threshold with rightward trunk rotation, although the post-hoc pairwise comparisons did not reach significance. The effect of trunk rotation on JND did not reach statistical significance ($F(2,38)=3.2$, $p=0.053$), albeit there was a trend for improved temporal sensitivity with rightward rotation (Fig. 3D).

Congruent saccade response: left-handed group

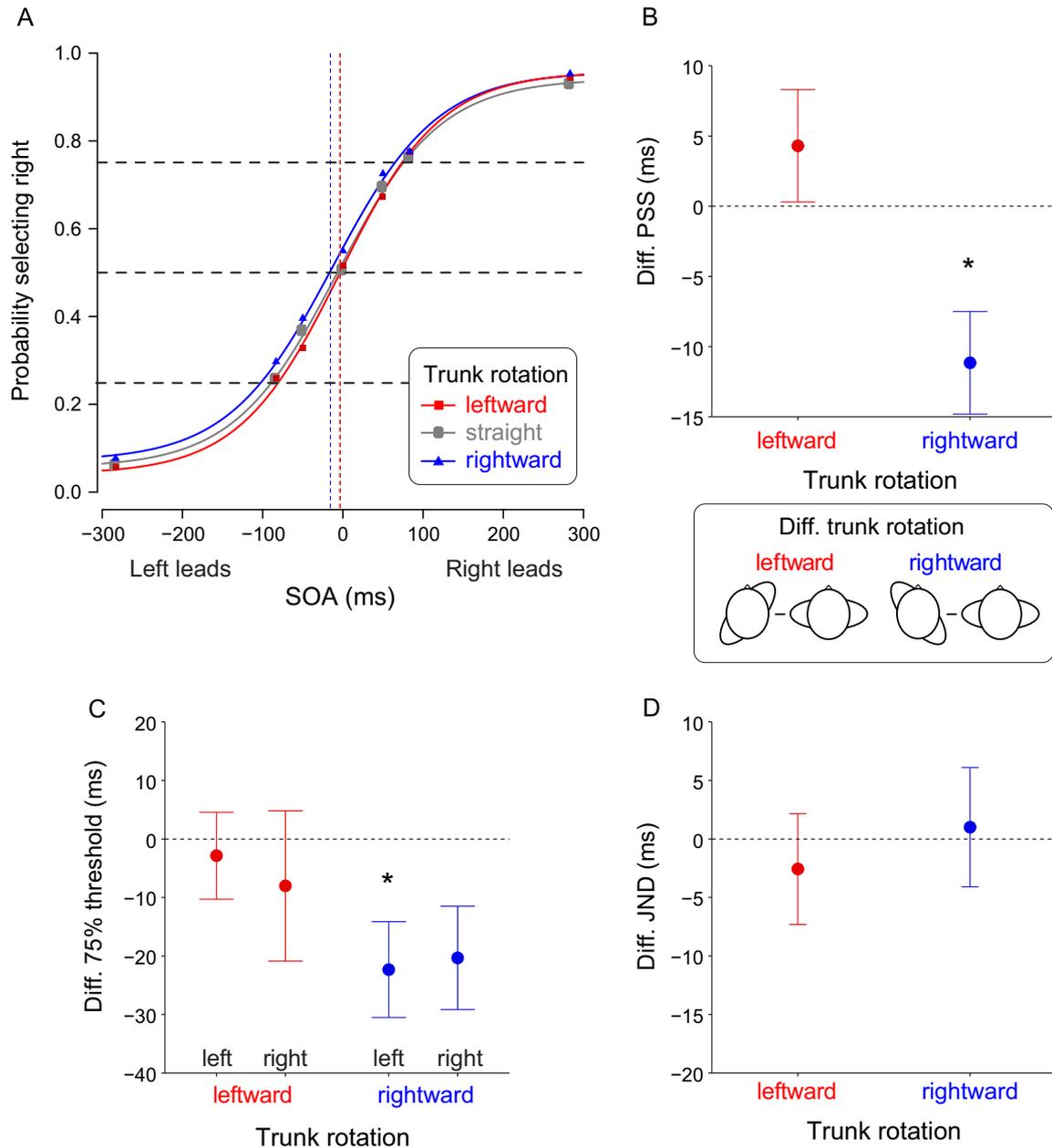


Fig. 4. Effect of trunk rotation on TOJ parameters in left-handed subjects. Same conventions as in Fig. 3. Stars in panels B and C denote significance at $p < 0.05$ for the post-hoc comparison of rightward rotation condition vs. straight condition.

3.2.2. Left-handed group

Fig. 4A illustrates the psychometric curves for left-handed subjects. Inspection of the psychometric functions indicated a shift due to trunk rotation. The rANOVA revealed a main effect of trunk rotation on PSS ($F(2,38)=6.8$, $p < 0.01$). Specifically, rightward trunk rotation led to an increase of right hemifield choices, as reflected in a negative value of differential PSS (Fig. 4B, mean differential PSS -11 ms). Conversely, leftward trunk rotation increased the PSS by 4 ms, reflecting a modest increase of left hemifield choices. Post-hoc pairwise comparisons performed for each trunk rotation indicated that rightward trunk rotation significantly differed from the straight and leftward trunk rotation ($p < 0.05$), while leftward trunk rotation did not significantly differ from the straight condition ($p=0.89$). Separate analysis of the

thresholds for 75% left and 75% right choices did not show an effect of trunk rotation on 75% right thresholds ($F(2,38)=1.7$, $p=0.2$). However, thresholds for left choices were significantly affected by trunk rotation ($F(2,38)=4.3$, $p < 0.05$). Post-hoc pairwise comparisons revealed that this effect was due to the shift of 75% left threshold to more negative SOA values with the rightward trunk rotation ($p < 0.05$), indicating that the stimulus in the left hemifield had to lead by 22 ms more to be chosen in 75% of trials. This effect is illustrated in Fig. 4C as the negative differential 75% left threshold. The effect of trunk rotation on JND was not significant ($F(2,38)=0.3$, $p=0.77$) (Fig. 4D).

To summarize the effects of trunk rotation in both handedness groups: (1) Rightward rotation induced a significant right choice bias in temporal order judgment in left-handed subjects;

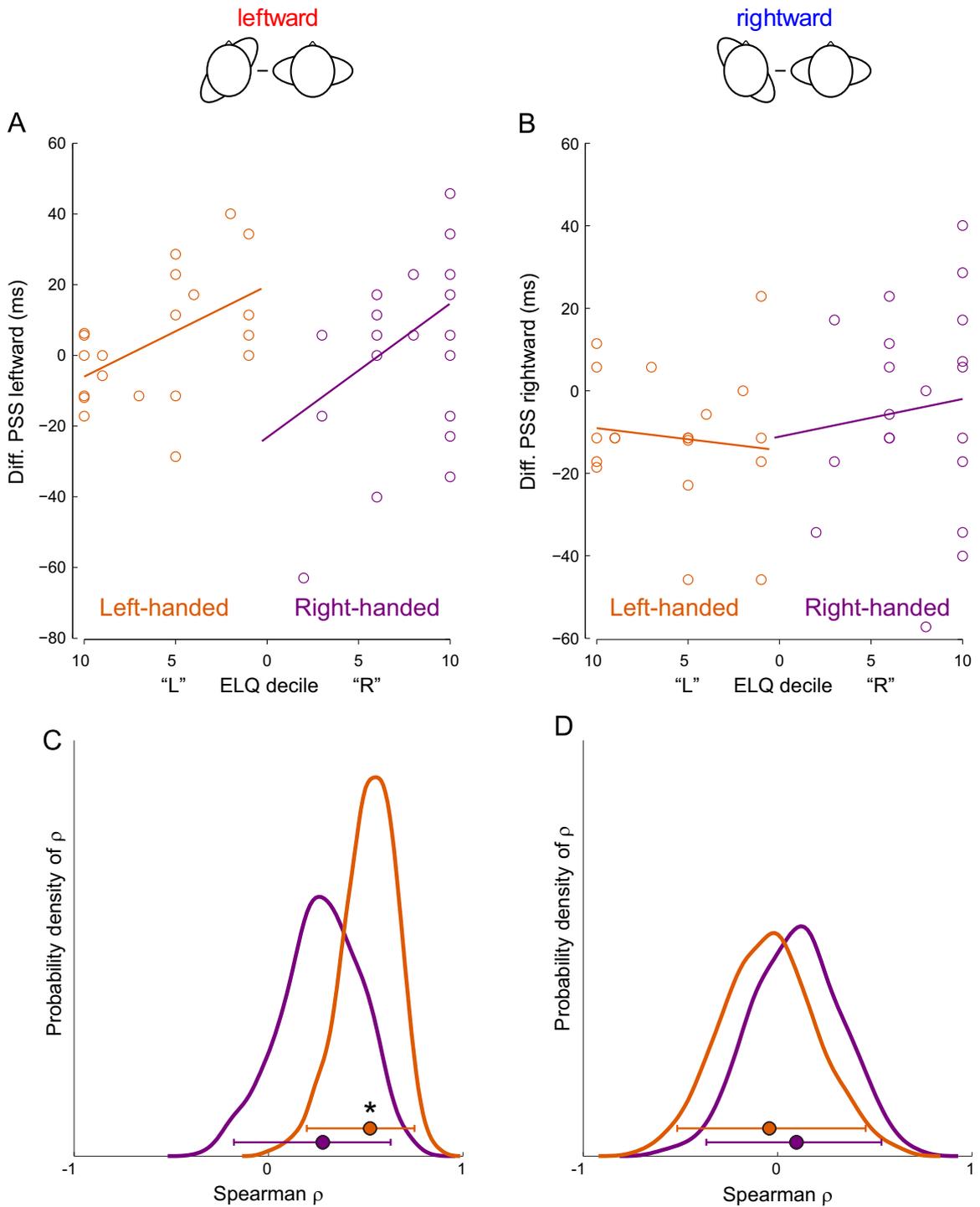


Fig. 5. Trunk-rotation dependent points of subjective simultaneity (PSS) as a function of degree of handedness. (A) Effect of *leftward* trunk rotation on PSS. Differential PSS is plotted against Edinburgh laterality quotient deciles (ELQ deciles, “L”-left-handed, “R”-right-handed). Data from individual right-handed and left-handed subjects are represented with purple and orange open circles, respectively. Solid lines represent best linear regression fit. (B) Effect of *rightward* trunk rotation on PSS. Same conventions as in (A). (C) Probability density distribution of Spearman correlation coefficients for data in panel A (leftward rotation), generated by a bootstrapping procedure (see Methods), and corresponding 95% confidence intervals, as indicated by 2.5–97.5% percentile range. Dot signifies 50% percentile. (D) Same conventions as in (C), for data in panel B (rightward rotation).

(2) Rightward rotation decreased the 75% choice thresholds, most pronounced in left-handed subjects. (3) Trunk rotation did not affect temporal sensitivity in either handedness group.

3.3. Influence of functional laterality on trunk rotation effects

Since laterality can be conceptualized as a continuous variable, we wondered whether trunk rotation effects on PSS vary as

a function of the degree of handedness. In order to test for this possibility, we correlated the differential PSS for leftward and rightward trunk rotations with the LQ deciles, separately for left- and right-handed groups. For the leftward trunk rotation, an observed positive correlation between differential PSS and LQ deciles in the right-handed subjects did not reach significance ($\rho=0.27, p=0.24$) (Fig. 5A and C). In contrast, left-handed subjects showed a significant positive correlation between

differential PSS and LQ deciles ($\rho=0.52$, $p<0.05$). A bootstrapping procedure (Section 2.5) further confirmed the significance of the positive correlation in the left-handed group (Fig. 5C). This correlation indicates that the less lateralized (i.e. more ambidextrous) left-handed subjects (LQ deciles L.5–L.1) exhibited a shift of PSS towards the left hemifield with leftward rotation (positive differential PSS), while strongly lateralized left-handed subjects mostly showed a weak PSS shift towards the right hemifield. For the rightward trunk rotation, there was no significant correlation in either group right-handed subject: $\rho=0.08$, $p=0.73$; left-handed subjects: $\rho=0.01$, $p=0.98$ (Fig. 5B and D).

Finally we tested, in left-handed subjects, if ocular dominance shapes the trunk rotation effect on temporal order judgments. The mixed ANOVA with the factors ocular dominance and trunk rotation on PSS revealed no interaction effect of ocular dominance, suggesting that the ocular dominance was not a major contributor to the effect of trunk rotation on the PSS (trunk rotation \times eye: $F(2,36)=1.08$, $p=0.35$).

3.4. Control experiment: effects of trunk rotation on temporal-order judgments with dissociated target-saccade locations

In the main experiment described above, subjects performed temporal order judgments with a congruent saccade response (rightward saccade for reporting right leading targets, and vice versa). Theoretically, the effect of trunk rotation could be due to

changes in perceptual performance, or due to a direction-specific saccade bias. In order to discriminate between these two possibilities, we conducted an additional control experiment, where the TOJ task remained the same, but the direction of the oculomotor response was dissociated from the target position and subjects indicated their response with an upward or downward saccade, according to a color association rule (Fig. 1C) (Section 2.4). We hypothesized that if trunk rotation leads to a motor, but not to a perceptual bias, the effect of trunk rotation on PSS would not be apparent when stimulus locations were dissociated from saccade target locations. This experiment was conducted in a randomly drawn subgroup of 10 right-handed and 10 left-handed subjects that had participated in the main experiment. When stimulus and saccade target location were dissociated, trunk rotation did not affect the proportion of right-first choices, as indicated by the lack of a significant main effect of trunk rotation in the ANOVA on PSS (right-handed: $F(2,18)=0.93$, $p=0.41$, left-handed: $F(2,18)=1.99$, $p=0.16$, Fig. 6A and B). Most importantly, the PSS results were also qualitatively different from the main experiment with spatially congruent saccades, yielding a trend towards positive differential PSS in the rightward trunk rotation in the left-handers in the incongruent task (Table 3).

Thus, when we disentangled the saccadic response from the stimulus hemifield location, no biasing effect towards the side of trunk rotation was observed in either right- or left-handed subjects.

Incongruent saccade response: right- and left-handed groups

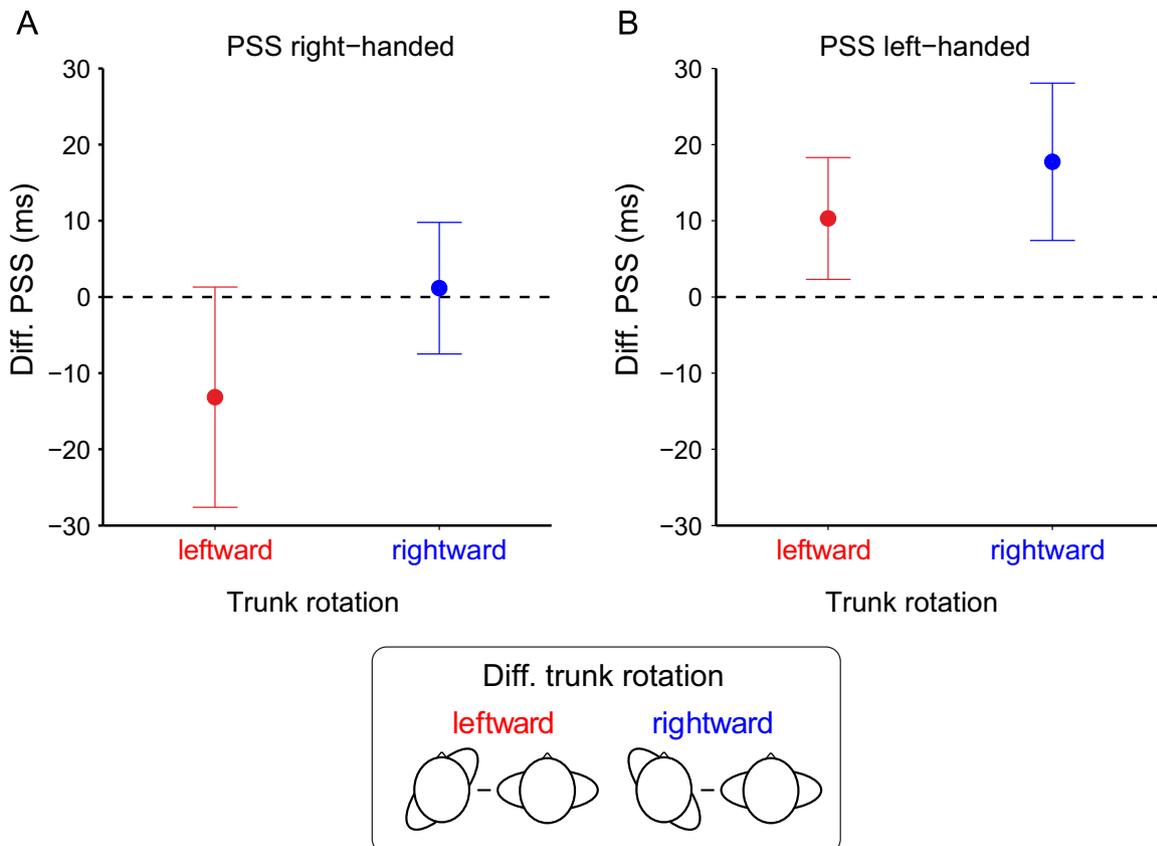


Fig. 6. Effect of trunk rotation on TOJ parameters in the control experiment with incongruent saccade responses. (A) Differential PSS ($PSS_{\text{leftward}} - PSS_{\text{straight}}$ and $PSS_{\text{rightward}} - PSS_{\text{straight}}$) as a function of trunk rotation for right-handed subjects. (B) Differential PSS ($PSS_{\text{leftward}} - PSS_{\text{straight}}$ and $PSS_{\text{rightward}} - PSS_{\text{straight}}$) as a function of trunk rotation for left-handed subjects. Means and S.E.M. across subjects are shown.

Table 3
Mean values and S.E.M. in ms for the control experiment with incongruent saccade responses.

Incongruent saccade task	Trunk rotation		
	Leftward	Straight	Rightward
Right-handed subjects			
PSS	–11 (15)	2 (10)	3 (10)
Threshold 75% left	–90 (25)	–79 (14)	–84 (15)
Threshold 75% right	76 (10)	84 (14)	90 (15)
JND	83 (15)	82 (9)	87 (13)
Left-handed subjects			
PSS	–11 (8)	–22 (13)	–4 (10)
Threshold 75% left	–94 (24)	–105 (22)	–74 (18)
Threshold 75% right	74 (15)	53 (14)	66 (13)
JND	84 (18)	79 (12)	70 (13)

4. Discussion

Using visual temporal order judgments (TOJ) we found that the point of subjective simultaneity in the straight trunk condition depends on both, handedness and ocular dominance. Trunk rotation effects were largest with rightward rotation, and in left-handed subjects, with effects having the same sign in right- and left-handers. Since TOJ bias towards the side of trunk rotation was only observed when subjects reported the leading target by a direct, congruent saccade, but were not present with incongruent saccade response locations, our results suggest that manipulation of the trunk midline primarily affects directed motor responses, while leaving the perceptual TOJ unchanged.

4.1. Spatial bias in the straight trunk condition as a function of handedness and ocular dominance

In the congruent TOJ task we found that right-handed subjects as a group tended to respond ‘right first’ when left and right stimuli were presented at the same time. This small right hemifield advantage in the right-handed population for visual TOJ tasks is known from the literature (Efron, 1963; Hirsh and Sherrick, 1961). Also the observation that the distribution of spatial bias in left-handed subjects was on average more symmetrical around zero is in accordance with previous studies using TOJ (Efron, 1963) or free viewing tasks (Ossandon et al., 2014). The rightward bias in right-handers (and accordingly slower processing for stimuli presented on the left side) in visual and somatosensory TOJ tasks has been hypothesized to result from a delay needed for transfer of signals from the right to the left hemisphere (Efron, 1963; Nicholls, 1994; Wada et al., 2004). In this context, the more symmetrical distribution of the point of subjective simultaneity in left-handed subjects has been attributed to less hemispheric specialization and thus the requirement of more extensive interhemispheric interactions in left-handed subjects (Wada et al., 2004). In support of this hypothesis, left-handers have on average greater bi-hemispheric representation of language than right-handers (Josse et al., 2006), and the corpus callosum in left-handers contains a higher number/density of axons as compared with right-handers (Westerhausen et al., 2004; Witelson, 1985). Also, interhemispheric transfer times, as measured by visually evoked potentials, show a directional asymmetry in right-handers (faster from the right to the left hemisphere), while being symmetric in left-handers (Iwabuchi and Kirk, 2009). However, there is also convincing evidence from recent fMRI studies in large samples of right- and left handed subjects that cast doubt on the predictive value of hand preference as a proxy for hemispheric lateralization for either language (Mazoyer et al., 2014) or spatial functions (Herve et al.,

2013; Petit et al., 2015). For example, studies employing Transcranial Doppler revealed that the majority of right- and left-handers (sometimes marked as ‘non-right handers’ to underline the continuous nature of handedness), show left hemisphere lateralization of language (95% and 75%, respectively) (Knecht et al., 2000), and predominance of spatial memory functions in the right hemisphere (both about 75%) (Whitehouse and Bishop, 2009). Most relevant for the current study, a recent fMRI study (Petit et al., 2015) that employed a visually guided saccade task in a large sample of 293 healthy subjects showed right hemispheric asymmetry in areas belonging to the ventral attention network irrespective of hand preference, and a right hemispheric asymmetry in fronto-parietal areas belonging to the dorsal attention network that was *more* pronounced in left-handers as compared to right-handers. Importantly, the same study also reported that the strongest rightward lateralization in fronto-parietal areas was observed in the group of left-handers with a preference for the right eye. Thus, the general view about a lesser degree of hemispheric specialization in left-handers might need revision and there might be also some interplay between ocular dominance and cerebral lateralization that has been dismissed in earlier studies (Carey, 2001; Mapp et al., 2003; Porac and Coren, 1976).

Our subject sample contained only 15% left-eye dominant right-handers, while 60% of the left-handers exhibited left-eye dominance. This association between manual preference and eye dominance is in agreement with previous studies (Annett, 2000; McManus et al., 1999; Petit et al., 2015). Unfortunately, the small number of crossed eye-hand dominance in the right-handed subjects made us focus the analysis of ocular dominance effects on the left-handed group. The direction of behavioral TOJ bias in the trunk straight ahead condition depended on ocular dominance. While left-handed subjects with a right ocular dominance showed a rightward TOJ bias, left-handed subjects with left ocular dominance showed a slight leftward bias. However, ocular dominance did not significantly mediate effects of trunk orientation, and it thus seems to be mainly an explanatory factor for an a priori spatial bias.

Although ocular dominance is not as well studied as handedness, previous studies suggested that inputs arriving from the dominant eye receive more visual attention and have a perceptual advantage (Shneur and Hochstein, 2006, 2008). For example, horizontal bias in line bisection tasks in healthy subjects is reduced by patching the dominant eye, suggesting that the initial bias during binocular viewing conditions is at least partly due to the dominant eye (Roth et al., 2002). Also, in neglect rehabilitation, ipsilesional eye patching has been shown to reduce hemispatial neglect symptoms in some patients (Butter and Kirsch, 1992), although evidence is not unequivocal (Smania et al., 2013; Soroker et al., 1994). Modulation of spatial bias following eye patching has been proposed to result from an activity decrease in the contralateral superior colliculus (SC) since, in contrast to cortical areas, the SC receives predominantly monocular input from the contralateral eye (Larsson, 2013). Consequently, a monocular patch would deprive the contralateral SC from its facilitatory visual input, which in turn reduces activity in the interconnected attention-related cortical areas within this cerebral hemisphere, leading to a bias in spatial orienting behavior (Smania et al., 2013). This idea is plausible given the evidence that the superior colliculus is an important node of spatial attention networks and is critically involved in both, the generation of visually-guided eye movements and target selection preceding the saccade (Himmelbach et al., 2007; Krauzlis et al., 2013; Opris and Bruce, 2005). Although this is speculative and little is known about the relationship between eye preference and neural activity patterns in spatial tasks (Bourassa et al., 1996), the right TOJ bias in right-sighted individuals might be explained as follows: The peripheral target in the right

hemifield activates the left superior colliculus first, which in turn activates the oculomotor network in the left hemisphere, leading to a reflexive saccade towards the right target.

Since ocular dominance has been so rarely taken into account, we propose that ocular dominance might account for some variability in behavioral and neural studies investigating spatial biases as a function of handedness. Nonetheless, the relationship between handedness, ocular dominance, and neural activity in attention- and oculomotor-related networks remains poorly understood and awaits future studies. For this reason, behavioral effects of handedness and ocular dominance need to be interpreted carefully in respect to underlying patterns of hemispheric asymmetries.

4.2. Effect of trunk rotation on spatial bias

Rightward trunk rotation caused a TOJ bias towards the right hemifield when target and saccade location coincided. This effect was more pronounced in left-handed subjects where it reached statistical significance. In contrast, leftward trunk rotation did not alter the saccade choice bias, although the biasing effect towards the left hemifield increased systematically in the left-handers with a decrease in the laterality quotient, i.e. with more usage of the right hand in daily life.

In the following section will discuss (1) How trunk rotation might interact with saccade planning signals on the neural level (2) Why rightward trunk rotation had a larger effect than leftward trunk rotation and why saccade choices in left-handed subjects were more susceptible to trunk rotation than in the right-handed group. (3) Lastly, we will discuss the dissociation between perceptual and motor-biasing effects of trunk rotation and the relation to previous studies in neglect patients and healthy subjects.

4.2.1. How trunk rotation interacts with saccade planning signals on the neural level

The interaction of neural activity related to visually-guided saccades and body postural signals has been documented for a multitude of multisensory brain regions in superior temporal and fronto-parietal cortices (Andersen, 1997; Cohen and Andersen, 2002; Colby, 1998). Evidence for this interaction is mainly derived from electrophysiological recordings and fMRI studies in non-human and human primates, respectively. In monkeys, trunk rotation has been shown to modulate the amplitude ('gain') of saccade-cue related responses of neurons in the lateral intraparietal sulcus (LIP) (Snyder et al., 1998). Interestingly, studies in fronto-parietal areas also showed effector-specific modulation such that some neurons in area LIP responded stronger to visual cues presented in the hemifield ipsilateral to the active hand (Oristaglio et al., 2006), and some neurons in FEF differentiate between congruent and incongruent target and hand position (Thura et al., 2011). Other putative sites for interactions between visual and proprioceptive afferents from the neck that have been reported in monkey electrophysiological and human imaging studies are the ventral intraparietal area (VIP) (Avillac et al., 2005), the polysensory parieto-insular vestibular cortex/temporoparietal junction (Fasold et al., 2008; Grusser et al., 1990; Karnath and Dieterich, 2006; Shinder and Newlands, 2014) and the motor and pre-motor cortices (Fasold et al., 2008; Wise et al., 1997). The shared circuitry of those multisensory brain regions that are modulated by proprioceptive postural signals is striking (Akbarian et al., 1992; Fasold et al., 2008; Karnath and Dieterich, 2006; Lopez and Blanke, 2011). The functional interrelationship between proprioceptive and visuomotor systems is further underlined by illusory perception of body rotation that is induced by vibratory stimulation of the posterior neck muscles (Goodwin et al., 1972) and by experiments showing effects of neck vibration on reaching (Biguer et al., 1988) and eye

movement behavior (Fujiwara et al., 2009). Furthermore, manipulation of neck proprioception by either physical or illusory trunk rotation-via neck vibration as well as vestibular stimulation by caloric irrigation into one ear or galvanic stimulation over the mastoid- have all been shown to change the subjective straight ahead as well as alleviate the rightward spatial bias in neglect patients, strongly suggesting, albeit not proving, a common underlying mechanism (Karnath et al., 1993, 1996; Moon et al., 2006; Rorsman et al., 1999; Schindler et al., 2002; Wilkinson et al., 2014).

In the context of the current study, we suggest that the effect of trunk rotation on spatial saccade choice bias is due to the facilitation of saccade target representations in the trunk rotation direction, possibly accompanied by inhibition of activity for targets in the opposite hemifield. Based on the neural studies outlined above, we assume that this activity modulation takes place in those brain regions that underlie the multimodal representation of space and integrate visual and body postural signals.

4.2.2. Larger effect of rightward trunk rotation than leftward trunk rotation

If right- and left-handed subjects were analyzed as one group, rightward trunk rotation facilitated saccade choices towards the right hemifield, while leftward rotation did not have an effect. Generally, saccade choices in left-handed subjects were more susceptible to trunk rotation than in the right-handed group. On the behavioral level, this could be explained by the fact that left-handers exhibit a greater degree of hand usage flexibility in everyday life, and thus the precise and flexible integration of postural parameters might be more important to them than for right-handers (Petit et al., 2015). This functional interpretation would be consistent with studies showing that left-handers represent body space more accurately than right-handers (Hach and Schutz-Bosbach, 2014; Linkenauger et al., 2009).

How can the different efficacy of rightward versus leftward trunk rotation possibly be explained on the neural level? The larger effect of right- as opposed to leftward trunk rotation is reminiscent of an earlier study reporting a facilitation of visual detection times for targets in the right visual hemifield, with minor effects with leftward trunk rotation (Hasselbach-Heitzeg and Reuter-Lorenz, 2002). At least three prior neuroimaging studies have used the proprioceptive equivalent of physical trunk rotation, i.e. vibratory stimulation of neck muscles. The first measured cerebral blood flow by PET together with left neck stimulation and reported activity increase in the right somatosensory cortex and insula and a decrease in the left fusiform and hippocampal gyrus (Bottini et al., 2001). Another fMRI study using right neck vibration reported activity increases within the same areas along with bilateral VIP, frontal eye fields and premotor cortex (Fasold et al., 2008). A third fMRI study, employing stimulation of the left neck muscles found increased activation in the left temporal lobe, with activation extending across the temporal gyri and the parahippocampal gyrus (Cutfield et al., 2014). However, none of the studies has directly compared the effects of left- and right neck vibration and their interaction with lateralized visual stimuli. Thus, those studies give valuable hints as to which brain regions are modulated by proprioceptive trunk input, but cannot resolve the stronger effects of rightward rotation found in our current study, nor do they provide a coherent picture about underlying hemispheric asymmetries.

There is strong evidence for an asymmetry of spatial representations from studies in neglect patients. Spatial neglect patients exhibit a strong bias to direct trunk, head and gaze towards the ipsilesional space (typically towards the right) along with attentional and perceptual deficits, which have been proposed to result from a lesion-induced deviation of the egocentric trunk midline towards the ipsilesional space (Fruhmann-Berger

and Karnath, 2005; Karnath, 1997; Ventre et al., 1984). Neglect symptoms occur more frequently and are more severe following stroke in the right hemisphere as compared with lesions in the left hemisphere (Kerkhoff, 2001). However, there is a surprising lack of knowledge about the occurrence of neglect symptoms in left-handers, as the large majority of studies explicitly focused on right-handed patients (Bareham et al., 2015). Thus, from the current neglect studies it remains unclear whether the predominance of left-sided neglect can be attributed to the fact that 90% of the population is right-handed and whether left-handed patients would show the reverse pattern, i.e. a right-sided neglect more frequently.

In any case, even if left-sided neglect should be more frequent than right-sided neglect independent of handedness, it seems paradoxical that rightward rotation should have a stronger effect in healthy subjects while only leftward trunk rotation has an effect on spatial bias in neglect patients (Karnath, 1994; Karnath et al., 1993, 1991). This apparent paradox can be resolved by adopting the transformation theory of left-sided neglect, that assumes a lesion-induced subjective shift of the egocentric trunk midline towards the ipsilesional (i.e. right) space that ultimately results in an ipsilesional (i.e. right) spatial bias (Karnath, 1997; Ventre et al., 1984). Albeit speculative, given the predominance of left-sided neglect, one may assume that a subjective shift of the trunk midline towards the right is more detrimental for spatial performance than a shift towards the left in both, lesioned and healthy subjects. Another, and not mutually exclusive explanation would be the assumption of a lateralized orienting gradient towards the right side of space in healthy subjects (Reuter-Lorenz et al., 1990). According to this view, the contralateral (i.e. left hemifield) bias of the right hemisphere is weaker than the corresponding contralateral (right hemifield) bias of the left hemisphere. This is consistent with previous studies suggesting that when spatial orienting conflicts are introduced, rightward bias becomes more robust than leftward bias (Reuter-Lorenz et al., 1990). In the current study, trunk rotation without concurrent head or gaze rotation could have acted as a source of conflict, which may have selectively strengthened the rightward bias. Alternatively, the stronger activation of the left hemisphere by rightward trunk rotation could have resulted in an amplification of an already existing rightward spatial bias via stronger activation of neurons coding for the right space in the left- or even in both hemispheres.

4.3. Dissociation between perception and action

Given that trunk rotation only affected TOJ bias when target and saccade location were congruent, but not when target and saccade report locations were incongruent, we conclude that trunk rotation did not affect perceptual performance, but interfered with the planning/generation of perceptually-contingent directed motor responses.

Convergent evidence from a multitude of behavioral, neurophysiological, and neuroimaging studies in animals, as well as in healthy and neurologically impaired humans suggests that the brain represents space in a variety of reference frames, some more related to goal-directed motor behavior (e.g. egocentric reference) and some more perceptual and abstracted from the body (e.g. allocentric, Cohen and Andersen, 2002; Humphreys et al., 2013). Likewise, it has been argued that the spatial choice bias in neglect patients could be either due to perceptual/attentional deficits or to a failure to perform a directional motor response, depending on lesion location (Harvey and Rossit, 2012). This notion is supported by lesion studies in humans and by inactivation studies in monkeys. Most relevant for the current study, patients with lesions in the parietal cortex showed an ipsilesional TOJ choice bias only when required to perform a directed saccade towards the first

appearing target, but not when they reported the temporal order of the targets with a button response (Ro et al., 2001). The authors interpreted this finding as an impairment of directed spatial motor responses, as opposed to conscious perception deficits, after parietal lesions. Similarly, pharmacological inactivation of the lateral bank of the intraparietal sulcus in monkeys has been shown to lead to spatial choice deficits in saccade tasks, while inactivation of the medial bank leads to spatial reaching bias (Kubaneck et al., 2015; Wilke et al., 2012). These results suggest effector-specific spatial choice computations in the parietal cortex. Most brain regions such as parietal and parieto-insular regions that have been previously reported to be modulated by physical trunk rotation and/or neck vibration (Fasold et al., 2008), belong to the 'dorsal pathway', that has been suggested to underlie directed visuomotor behavior without the need for conscious perception (Westwood and Goodale, 2011). Following this reasoning, we interpret the TOJ bias towards the side of trunk rotation that was observed in our study, as direction-specific facilitation of oculomotor responses, possibly induced by gain-field modulation of parietal neurons.

The current state of studies in healthy subjects presents a rather incoherent picture in the framework of perceptual vs. motor effects of trunk rotation: Grubb and Reed employed a covert attention task that required 18 subjects to report the side at which the target had appeared by pressing the corresponding left or right mouse button (Grubb and Reed, 2002). They reported that leftward trunk rotation increased reaction times for invalidly cued targets in the right hemifield. Since target side and motor response were congruent, these results could in theory be explained by directional response priming. However, a subsequent study could not reproduce the result from Grubb and Reed (Chen and Niemeier, 2014). The latter study also ruled out possible confounding factors that could have explained the discrepancy between the two studies, such as gender bias, small eye movements and subject sample size (Chen and Niemeier, 2014). Reminiscent of the larger effects for rightward rotation in our current study, Hasselbach-Heitzeg and Reuter-Lorenz found a decrease in detection times and an increase in visual sensitivity for right lateralized luminance targets when the trunk of 12 healthy right-handed subjects was rotated rightwards, but no effect for left rotation (Hasselbach-Heitzeg and Reuter-Lorenz, 2002). Furthermore, in this study, the button for 'yes' and 'no' target reports was randomized and the location was indicated by verbal report. Thus, the trunk rotation effects of this study can hardly be reduced to the facilitation of a directed motor response. Another study that tested the proprioceptive equivalent of trunk rotation in 6 subjects did not find an effect of (left) neck vibration on TOJ judgments (Rorden et al., 2001). Although this study used spatially congruent (left vs. right) button responses, responses were not speeded and might thus have been biased towards perceptual representations. Taken together, the previous studies in healthy subjects do not explicitly support the hypothesis that trunk rotation effects are larger for fast and directed motor responses, but do not defy this hypothesis either. The studies cited above used button responses, while we employed either spatially congruent or incongruent speeded saccade responses, which might be even more sensitive to automatic orienting responses. To resolve these discrepancies and questions, future studies would profit from making the full dissociation between effectors (saccade vs. reaching) and spatial response compatibility.

A previous study in monkeys investigated the effect of trunk rotation on TOJ with direct saccades (Scherberger et al., 2003). Unlike our results, this study did not find an effect of trunk rotation on saccade target selection. There are several possible reasons for the lack of trunk-rotation effect in the Scherberger et al. study: (1) Monkeys do not exhibit strong hemispheric lateralization for spatial functions (Kagan et al., 2010), (2) The maximal trunk

rotation used in this study was only 16° (while being more extreme in our study) (3) Monkeys were possibly over-trained on the task, thus showing more robust performance levels with all experimental manipulations. (4) Saccade trials were interleaved with reach trials, and central hand fixation was required during saccades, thus possibly re-centering the spatial attention and counteracting egocentric midline shifts. (5) Monkeys were rewarded equally for either choice, while human subjects were explicitly instructed to indicate the first stimulus, and were rewarded according to their (correct) performance. Further experiments, matching task design and behavioral context, are needed to resolve if there is a systematic difference between species in this regard.

In conclusion, our results suggest that egocentric midline shifts primarily affect TOJ in the context of directed motor responses. In addition, our findings underline the importance of taking individual differences in functional laterality such as handedness and ocular dominance, as well as the mode of perceptual report into account when evaluating effects of trunk rotation in either healthy subjects or neurological patients.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.neuropsychologia.2015.10.031>.

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