

Role of oculoproprioception in coding the locus of attentionBartholomaeus Odoj^{1,2} and Daniela Balslev³

¹*Center of Neurology, Division of Neuropsychology, Hertie Institute for Clinical Brain Research, University of Tuebingen, Tuebingen, 72076, Germany*

²*Department of Psychology, University of Copenhagen, Copenhagen, DK-1353, Denmark*

³*School of Psychology and Neuroscience, University of St Andrews, St Andrews, KY169JP, UK*

Running title: Oculoproprioception in spatial attention

Correspondence:

Daniela Balslev
School of Psychology and Neuroscience
University of St Andrews
St Mary's Quad
South Street
St. Andrews
KY16 9JP
United Kingdom
phone +44 (0)1334 462097
fax +44 (0)1334 463042
daniela.balslev@st-andrews.ac.uk

Abstract

The most common neural representations for spatial attention encode locations retinotopically, relative to center of gaze. To keep track of visual objects across saccades or to orient towards sounds, retinotopic representations must be combined with information about the rotation of one's own eyes in the orbits.

Although gaze input is critical for a correct allocation of attention, the source of this input has so far remained unidentified. Two main signals are available: corollary discharge (copy of oculomotor command) and oculoproprioception (feedback from extraocular muscles). Here we asked whether the oculoproprioceptive signal relayed from the somatosensory cortex contributes to coding the locus of attention. We used continuous theta burst stimulation (cTBS) over a human oculoproprioceptive area in the postcentral gyrus ($S1_{EYE}$). $S1_{EYE}$ cTBS reduces proprioceptive processing, causing $\sim 1^\circ$ underestimation of gaze angle. Participants discriminated visual targets whose location was cued in a non-visual modality. Throughout the visual space, $S1_{EYE}$ cTBS shifted the locus of attention away from the cue by $\sim 1^\circ$, in the same direction and by the same magnitude as the oculoproprioceptive bias. This systematic shift cannot be attributed to visual mislocalization. Accuracy of open-loop pointing to the same visual targets, a function thought to rely mainly on the corollary discharge, was unchanged. We argue that oculoproprioception is selective for attention maps, and that it helps align attention loci to the space of the body. By identifying a potential substrate for the coupling between eye and attention, this study contributes to the theoretical models for spatial attention.

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Keywords

Human, Proprioceptive, Somatosensory, Spatial Attention, Transcranial Magnetic
Stimulation, Visual

For Review Only

Introduction

Attention allows organisms to focus on relevant stimuli. In monkeys, neurons that respond to attended stimuli have a retinotopic receptive field, which reference location relative to the direction of gaze (Andersen & Mountcastle, 1983; Gottlieb, Kusunoki, & Goldberg, 1998). A retinotopic code for attended stimuli has also been observed in humans. Indeed, although visual perception is normally facilitated at the location indicated by an attention cue, just after an eye movement, attention can be transiently allocated away from the cue, at its previous retinotopic coordinates (Golomb, Chun, & Mazer, 2008; Golomb, Nguyen-Phuc, Mazer, McCarthy, & Chun, 2010; Mathôt & Theeuwes, 2010; Talsma, White, Mathôt, Munoz, & Theeuwes, 2013).

Retinotopic representations alone cannot support cross-modal interactions in spatial attention between visual and non-visual modalities or maintain a stable focus of attention across eye movements. One solution to this problem could be to create coregistered representations in multiple reference frames (Andersen, Snyder, Bradley, & Xing, 1997; Pouget, Deneve, & Duhamel, 2002). Another solution could be to update the retinotopic representation for each eye movement (Duhamel, Colby, & Goldberg, 1992). Importantly, both solutions require information about the rotation of the eyes in the orbits. Despite the importance of the gaze information in the brain's representations for spatial attention, the sources of this gaze input to the attention maps remain unknown. The main sources of eye position are the feedback from the extraocular muscles or oculoproprioception (Sherrington, 1918) and an internal model that predicts future eye rotation based on the copy of the oculomotor command or corollary discharge (von Helmholtz, 1925).

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3 Does oculoproprioception play a role in coding the locus of attention? On the one
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5 hand, some studies fail to find a decrease in accuracy or precision of visual
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7 localization in conditions when oculoproprioception is reduced or abnormal (Balslev,
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9 Himmelbach, Karnath, Borchers, & Odoj, 2012; Guthrie, Porter, & Sparks, 1983;
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11 Lewis, Gaymard, & Tamargo, 1998). Such findings support the suggestion that
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13 oculoproprioception does normally not contribute to the estimate of eye rotation, but
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15 rather calibrates the oculomotor command in the long-term, i.e. days (Steinbach,
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17 1986; Wurtz, 2008).

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20 On the other hand, some behavioural studies (Golomb et al., 2008, 2010; Mathôt
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22 & Theeuwes, 2010; Talsma et al., 2013) show delays in updating the retinotopic
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24 coordinates where attention is deployed after a saccade. These delays are compatible
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26 with the delay in the ascending fibres (Wang, Zhang, Cohen, & Goldberg, 2007; Y.
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28 Xu, Wang, Peck, & Goldberg, 2011) and therefore leave open the possibility that
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30 oculoproprioception may contribute. Furthermore, we have observed alterations in
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32 visual sensitivity in conditions that distort the oculoproprioceptive signal. The
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34 oculoproprioceptive signal was distorted in the ocular periphery, using passive eye
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36 rotation (Balslev, Newman, & Knox, 2012), or centrally, in the somatosensory cortex,
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38 after applying repetitive transcranial magnetic stimulation (Balslev, Gowen, & Miall,
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40 2011; Odoj & Balslev, 2013) or after a focal lesion (Balslev, Odoj, & Karnath, 2013) .
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42 These previous studies suggest a link between the the oculoproprioceptive signal in
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44 the somatosensory cortex and spatial attention, however, the nature of this link is still
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46 unclear. One possibility is that the *attention* map incorporates oculoproprioception, so
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48 that a distorsion of this signal causes a systematic shift in the locus of attention
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50 relative to a cue. Another possibility is that the *visual* map incorporates
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52 oculoproprioception, so that a distorsion of this signal cause a systematic error in
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3 locating visual targets relative to the body. Visual stimuli presented nearer the hand
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5 (Reed, Grubb, & Steele, 2006), the head midline (Durand, Camors, Trotter, &
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7 Celebrini, 2012; Jean-Baptiste Durand, Trotter, & Celebrini, 2010), or the trunk
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9 midline (Grubb, Reed, Bate, Garza, & Roberts, 2008) have a privileged access to
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11 neural processing resources compared to visual stimuli presented elsewhere. A
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13 mislocalization of the visual stimuli relative to these landmarks could, in our previous
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15 studies, have changed their neural processing priority.
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18 Here, we investigated whether oculoproprioception is incorporated in attention
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20 maps..
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23 Oculoproprioception was manipulated using continuous theta burst stimulation
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25 (cTBS), a form of inhibitory transcranial magnetic stimulation, over an
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27 oculoproprioceptive area in the human postcentral gyrus ($S1_{EYE}$). Inhibitory repetitive
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29 transcranial magnetic stimulation over $S1_{EYE}$ interferes with the ability to correct for
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31 passive eye movement during a visual localization task (Balslev & Miall, 2008) and
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33 results in an underestimation of the rotation of the eye in the orbit by $\sim 1^\circ$ (Odoj &
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35 Balslev, 2013). We used $S1_{EYE}$ cTBS over the left postcentral gyrus to alter the
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37 oculoproprioceptive signal. Participants discriminated visual targets whose location
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39 was cued by the position of their unseen left index finger, or pointed to these targets
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41 using the same finger. Both tasks depend critically on eye position information, to
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43 match the location of the visual target with the location of the finger that acted as
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45 either a cue or as an effector.
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49 We report a systematic error in the locus of attention and no pointing error
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51 after $S1_{EYE}$ -cTBS. We argue therefore that oculoproprioception is the eye position
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53 signal that anchors attention loci in the visual space to the body.
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Methods

Overview of the experiments

Experiment 1 examined the allocation of attention using a cross-modal task. Participants discriminated a visual target. The location of this target was cued by the location of the unseen left index finger. The locus of attention was defined as the location in the visual space where the cue had the largest effect on the reaction time for target discrimination. If oculoproprioception is incorporated into the attention maps, one would predict a systematic error in the locus of attention relative to the location of the cue after $S1_{EYE}$ -cTBS.

Experiment 2 examined visuospatial localization using an open-loop pointing task. Participants used their unseen left index finger to reach to visual targets, in the absence of visual feedback. If oculoproprioception is incorporated into visual maps, one would predict a systematic error in open loop pointing after $S1_{EYE}$ -cTBS.

Experiment 3 examined participants' ability to locate their unseen left index finger using an open loop pointing task. This experiment controlled for an effect of $S1_{EYE}$ -cTBS on the ability to locate the non-visual cue in Experiment 1.

All experiments were conducted with the participants fixating rightward (Experiments 1A-3A) and leftward (Experiments 1B-3B). The reason for repeating the experiment for different directions of gaze was the following. The effect of $S1_{EYE}$ -cTBS on visual localization is gaze dependent, i.e. a shift in perceived eye rotation towards left in rightward gaze and towards right in leftward gaze (Odoj & Balslev, 2013), reflecting the underestimation of the rotation of the eyes in the orbits. We predicted therefore that the change in the direction of gaze would reverse the effect. In

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3 this way, one can separate a specific, gaze-dependent effect, from a general influence
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5 of anterior parietal cortex on attention (Experiment 1) or reaching (Experiments 2-3).
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8 9 *Participants*

10 We tested 10 participants (5 female) in each of three different experiments
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12 (Experiments 1-3). All were right-handed with normal or corrected to normal vision.
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14 For experiments 1A-3A, participants had an age range from 22 to 32 years (median:
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16 28.5 years). For experiments 1B-3B participants had an age range from 27 to 32 years
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18 (median: 29 years). Five participants took part in all experiments (A and B). All
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20 participants gave their informed consent. The study was approved by the local Ethics
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22 Committee at the University of Tuebingen.
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30 *Experiment 1. Attention map*

31 This experiment investigated whether oculoproprioception is included in the eye
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33 position estimate necessary for orienting attention in the visual space in response to a
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35 non-visual cue.
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38 Participants discriminated a target (letter “A” or “H”, size 1° visual angle) whose
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40 most probable location was indicated by a somatosensory cue, the location of the
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42 participant’s left index finger hidden from view. We assumed that cTBS of the
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44 ipsilateral, left somatosensory cortex will have only a small effect, if any on
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46 perceiving finger location. This assumption was explicitly tested in Experiment 2. The
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48 experimenter placed the participant’s index finger just below the horizontal line where
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50 targets were presented. To assess the benefit of the cue, we calculated the difference
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52 in reaction time for visual discrimination in the presence vs. the absence of the cue.
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54 The locus of attention was the location with the largest benefit of the cue. 'Cueing
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3 error' was defined as the difference between the locus of attention and the actual
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5 location of the cue. If eye proprioception contributes to coding the locus of attention,
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7 S1_{EYE}-cTBS should increase cueing error, by causing a shift the locus of attention
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9 away from the cue and towards the center of the orbit, in the same direction as the
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11 shift in perceived eye position.
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16 *Setup*

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21 *Insert Figure 1 about here*
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23 Participants sat with their head fixed in a chin rest and cheek pads. A cathode ray tube
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25 (CRT) display was placed at 45 cm in front of them (Figure 1 A). The CRT was
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27 centered at +19° (Experiment 1A) or at -19° (Experiment 1B, Figure 1) from center of
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29 the right orbit. Participants performed the task in right eye vision, with the left eye
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31 patched. The experiment was conducted in monocular vision for the following reason.
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33 In the macaque, the primary oculoproprioceptive area 3a receives proprioceptive
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35 information from the contralateral eye only (Wang et al., 2007). In humans, although
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37 proprioceptive information from both eyes is relayed to each brain hemisphere
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39 (Balslev, Albert, & Miall, 2011), the input from the contralateral eye is functionally
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41 more important (Balslev, Himmelbach, Karnath, Borchers, & Odoj, 2012). Therefore
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43 we assumed that after cTBS of one hemisphere (left), the effects would be strongest
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45 and easier to measure for the contralateral eye (right). As a somatosensory cue we
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47 used the position of the participants' left index finger, ipsilateral to the hemisphere
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49 where TMS was applied. A transparent (Plexiglas) sheet was mounted 5 cm in front
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51 of the CRT screen. Participants had their left index finger on a support (a wooden
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53 ledge) attached to the Plexiglas immediately under the location where the targets
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3 would appear. The finger was placed at one out of four possible cue positions, 8°, 18°,
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5 20° or 30° to the right (Experiment 1A, rightward gaze) or left (Experiment 1B,
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7 leftward gaze) from orbit midline of the right eye and covered with black cloth by the
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9 experimenter. The experiment took place in total darkness. The participants had no
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11 visual information about finger location (somatosensory cue), to prompt the use of
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13 gaze information to locate the visual targets relative to the cue.
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17 At the beginning of the trial, participants fixated on a central cross (white,
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19 1°×1°) presented on black background (Figure 1B). Fixation was verified with a head-
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21 mounted eye tracker (EyeLinkII). After 500-650 ms (randomized) the fixation cross
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23 disappeared. 100 ms later, a target letter ('A' or 'H', 1° visual angle) appeared for 100
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25 ms. The target appeared at 1 out of 7 possible locations, at -3°, -2°, -1°, 0°, 1°, 2°, 3°
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27 from the somatosensory cue. Participants were told that the target letter is most likely
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29 to appear at the location indicated by the cue. The target letter was however presented
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31 with equal probability (8 times) at each of the seven possible target locations.
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33 Additionally, three trials showed target letters at random locations outside this range
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35 so that the participants could not predict the location of the non-visual cue from the
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37 spatial distribution of the visual targets. The participants were instructed to name the
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39 target letter as fast and accurately as possible. Voice reaction time (VRT) was
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41 recorded.
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46 Trials with the same cue location were grouped in blocks. Each block
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48 consisted of 59 trials (8 trials for each of the 7 target positions + 3 random positions).
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50 Trial order was pseudo-randomized. At the end of each block, participants were
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52 instructed to close their eyes. Then the experimenter moved the participants' index
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54 finger at the next cue location and started a new block. The participants completed 4
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56 cued blocks (cue at +8°, +18°, +20° or +30° degree from orbit midline in Experiment
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3 1A and -8° , -18° , -20° or -30° in Experiment 1B). The order of the blocks was
4
5 pseudo-randomized.

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7 To assess the baseline distribution of attention as well as visual accuracy,
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9 participants performed the same visual discrimination task in the absence of a cue.
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11 Participants' left index finger rested in front of their body midline. Target letters were
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13 presented on the screen at all locations tested in the cued blocks. These locations were
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15 probed in random order, 4 times each. The uncued block consisted of 92 trials. This
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17 block was performed either before or after the cued blocks, randomized across
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19 participants.
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25 26 *Data analysis*

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28 We calculated the difference in reaction time for visual discrimination in the presence
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30 versus the absence of the cue. The locus of attention was the location with the largest
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32 benefit of the cue (the largest decrease in reaction time in the presence vs. the absence
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34 of the cue). The cueing error was calculated as the difference between the locus of
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36 attention and the location of the cue (Figure 2).
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42 *Insert Figure 2 about here*
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48 Cueing error for each cue location was compared before and after cTBS using paired-
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50 samples t-tests. Mean cueing error was analyzed using a repeated-measures ANOVA
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52 with factors (1) TMS run (pre vs. post), (2) stimulation area (S1_{EYE} vs. P3) and (3)
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54 gaze direction (leftward vs. rightward). If oculoproprioception is incorporated into
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56 attention maps, one would predict a significant 3-way interaction, driven by an
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3 increased cueing error after $S1_{EYE}$ -cTBS. The cueing error was expected to have
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5 opposite sign for leftward and rightward gaze, mirroring the underestimation of the
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7 angle of gaze after $S1_{EYE}$ -cTBS (Experiment 1 in Odoj & Balslev, 2013) .
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10 To assess whether the results are robust, we repeated the analysis using a different
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12 method for calculating the locus of attention. We now defined the locus of attention as
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14 the center of mass of all locations that showed a cueing benefit. First, we identified all
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16 locations showing a benefit of the cue, indicated by a faster reaction time with than
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18 without the cue. Then, we calculated the mean of these locations, after weighting each
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20 location with the magnitude of the cueing effect there. To separate out an eventual
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22 practice effect (i.e an improvement of reaction time that was common to all target
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24 locations within a block), we pre-processed the data by subtracting the mean RT for
25
26 each block of trials.
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29 30 31 32 *Experiment 2. Visual map*

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34 Experiment 2 examined the ability to locate visual targets relative to the left index
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36 finger after $S1_{EYE}$ -cTBS using a pointing task. This experiment also controlled for an
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38 error in hand proprioception after cTBS in the postcentral gyrus. This allowed to rule
39
40 out a systematic error in the perception of the non-visual cue in Experiment 1.
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43 Participants pointed with their left index finger, the same finger which was used as a
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45 non-visual cue in Experiment 1. Visual targets were presented at the same locations
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47 as the cues in Experiment 1. If locating visual targets for reaching takes
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49 oculoproprioception into account or if cTBS of the left postcentral gyrus alters
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51 perceived posture of the ipsilateral hand, one would expect pointing errors after
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53 $S1_{EYE}$ -cTBS.
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Setup

The setup was identical with that used in Experiment 1. Additionally, a position sensor (Polhemus Fastrak) was fixed on the tip of the participants left index finger.

Insert Figure 3 about here

At the beginning of the trial, the participants fixated on a central cross ($1^\circ \times 1^\circ$, white on black background). Fixation was verified with the head-mounted eye tracker. Participants' left index finger rested in front of their body midline (Figure 3 A). After 500-650 ms (randomized) the fixation cross disappeared. 100 ms later, a target letter ('X') appeared for 100 ms. The target could appear at 4 possible locations: at 8° , 18° , 20° or 30° from orbit midline in Experiment 2A, or at -8° , -18° , -20° or -30° from orbit midline in Experiment 2B. The participants were instructed to close their eyes, then point with their left index finger as accurately as possible at the remembered location of the target. The reaching movement stopped on the wooden ledge, when the finger touched the plexiglass. Participants were allowed to adjust the position of their finger until they felt the finger was pointing to the target. After participants confirmed that this was the case, finger position was recorded and the experimenter moved the finger back to the resting position at body-midline. Trials for each target position were grouped in blocks. Each block consisted of 6 trials. Block order was pseudo-randomized.

Data analysis

Pointing error was calculated as the signed difference between target and finger location at the end of the movement. Pointing error for each target location was compared before and after cTBS using paired-samples t-tests. Mean pointing error

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3 across all target locations was analyzed using a repeated-measures ANOVA with
4 factors (1) TMS run (pre vs. post), (2) stimulation area (S1_{EYE} vs. P3) and (3) gaze
5 direction (leftward vs. rightward). If oculoproprioception is incorporated into visual
6 maps, one would predict a significant 3-way interaction, driven by an increased
7 pointing error after S1_{EYE}-cTBS. The pointing error was expected to have opposite
8 sign for leftward and rightward gaze, mirroring the underestimation of the angle of
9 gaze after S1_{EYE}-cTBS (Experiment 1 in Odoj & Balslev, 2013) .
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20 *Experiment 3. Perceived finger posture*

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22 Experiment 1 required to match the position of the unseen finger at rest with a visual
23 target, whereas Experiment 2 asked participants to point the same finger at a visual
24 target without visual feedback. One could explain a systematic cueing error in
25 Experiment 1 despite accurate open-loop pointing in Experiment 2 by an error in the
26 perceived posture of the left index finger at rest. To investigate whether S1_{EYE}-cTBS
27 selectively disturbs the felt position of the left index finger at rest (rather than during
28 movement), we conducted a third experiment. In this experiment participants were
29 asked to point with the left index finger to the remembered position of this finger. The
30 participants had their eyes closed, and thus no visual feedback. We measured pointing
31 error as the difference between the location of finger at the end of movement and the
32 location where the left index finger was passively placed.
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48 The setup was identical with Experiment 2. At the beginning of each trial, the
49 experimenter took the participant's left index finger from the starting position in front
50 of the body-midline and placed it at one out of the four possible locations, identical to
51 the target locations from Experiment 2 and the cue locations from Experiment 1. After
52 1 second, the index finger was moved back to start position. Then the participants
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3 were instructed to point to the remembered location of their finger as accurately as
4 possible. They confirmed verbally, when they reached this location. The experimenter
5 recorded the coordinates of the fingertip and moved the participants' finger back to
6 the start position. Trials for each of the four target position were grouped in blocks.
7 The target was presented 6 times within one block. The order of the blocks was
8 randomized. If S1_{EYE}-cTBS affect perceived position of the left index finger at rest,
9 but not during movement, then one would predict a pointing error in this experiment
10 after S1_{EYE}-cTBS.
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22 *TMS*

23 A standard 70-mm-diameter figure-of-eight coil centered over the stimulation site was
24 fixed in place by a coil holder. The participant's head was restrained by a chin rest.
25 We followed an identical procedure for locating S1_{EYE} as in previous studies
26 conducted by Balslev and colleagues (Balslev, Gowen, et al., 2011; Balslev & Miall,
27 2008; Odoj & Balslev, 2013). S1_{EYE} was mapped in each participant in relation to the
28 “motor hotspot” of the left hemisphere, which is the scalp projection of the primary
29 motor cortex for the hand (M1). The motor hotspot was defined as the point of
30 maximum evoked motor response in the first dorsal interosseous muscle of the right
31 hand. The S1_{EYE} site of stimulation was located at 3 cm posterior to the motor hotspot,
32 measured on a line oriented at 45° from the sagittal plane and perpendicular on the
33 central sulcus.
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49 Post hoc neuronavigation has showed that that this coil location targets an area
50 in the postcentral gyrus, at MNI coordinates (-45±7, -32±7, 58±9) (mean±SD)
51 (Balslev, Siebner, Paulson, & Kassuba, 2012). The mean coordinate is associated with
52 a probability of 46% for area 3b, 37% for area 1 and 27% for area 2 according to the
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3 probabilistic stereotaxic cytoarchitectonic atlas of the Anatomy Toolbox v2.1
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5 (Eickhoff et al., 2005). The underestimation of the angle of gaze after S1_{EYE}-cTBS
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7 for both left and right directions of gaze(Experiment 1 in Odoj & Balslev, 2013)
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9 suggest that S1_{EYE} is organized like the primary oculoproprioceptive area 3a in the
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11 macaque, where neurons encode gaze angle for all directions of gaze (Wang et al.,
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13 2007) It is unlikely that TMS applied over the scalp can reach area 3a, located in the
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15 depth of the central sulcus (Geyer, Schleicher, & Zilles, 1999). The center-periphery
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17 principle of organization however, may be common to all neural populations that
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19 receive an oculoproprioceptive projection. These neural populations are not limited to
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21 the depth of the central sulcus, but extend into the postcentral and precentral gyri
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23 (Balslev, Albert, & Miall, 2011).
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27 During stimulation, the coil was positioned tangential to the scalp with the long axis
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29 of the figure-of-eight coil oriented at 45° to the parasagittal plane. The current flow of
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31 the initial rising phase of the biphasic pulse in the TMS coil induced a current flowing
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33 from posterior to anterior in the brain. On the basis of the decreased amplitude of the
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35 somatosensory-evoked potentials after cTBS over a region situated at 2 cm posterior
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37 to M1 (Ishikawa et al., 2007), we assumed that cTBS over S1_{EYE} results in a
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39 decreased excitability of this area. The control site of stimulation in the parietal lobe,
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41 P3, was located by using the International 10-20 system for EEG placement. Hilgetag
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43 and colleagues found that repetitive TMS over P3 improves visuospatial attention in
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45 the ipsilateral hemifield (Hilgetag, Theoret, & Pascual-Leone, 2001). Therefore we
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47 chose this area as control region to check if a possible effect, found in S1_{EYE}-cTBS,
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49 could be explained by a spread of the induced current from S1_{EYE} towards P3. cTBS
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51 consisted of 600 biphasic stimuli produced by a Magstim Rapid² stimulator. They
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53 were delivered with a frequency of three pulses at 50 Hz repeated at 200 ms (5 Hz)
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3 for 40 s. The stimulation intensity was set at 80% of active motor threshold of the
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5 right first dorsal interosseous (Huang, Edwards, Rounis, Bhatia, & Rothwell, 2005).
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7 For each experiment, participants underwent two sessions, with cTBS at either S1_{EYE}
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9 or the control site (P3). The order of the sessions was randomized across participants
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11 and scheduled on separate days. During each session, the participant was tested before
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13 (pre-cTBS) and after (post-cTBS) on an identical task. Data collection was completed
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15 within 13 min after the cessation of the stimulation, a time interval for which the
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17 inhibitory aftereffect of cTBS in the somatosensory cortex has been demonstrated
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19 (Ishikawa et al., 2007).
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25 *Eye Tracking*

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27 The position of the right eye was recorded with a head mounted tracker
28
29 (EYELINK II, SR Research Ltd., Ottawa, Canada) that sampled pupil location at 250
30
31 Hz. The tracker was calibrated after each cTBS run (pre- or post-cTBS) using a 3 × 3
32
33 grid.
34
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36 Eye position time series were parsed into fixations, blinks, and saccades using
37
38 the SR EyeLink detection algorithm, which was set to detect saccades with an
39
40 amplitude of at least 0.5°, using an acceleration threshold of 9500°/sec² and a velocity
41
42 threshold of 30°/sec, and then analyzed off-line. Trials with a mean deviation of more
43
44 than 1.5° from fixation within 50 ms before target presentation were discarded. In
45
46 experiment 1 a total of 10.8 ± 7.7% (mean ± standard deviation) trials were discarded.
47
48 In experiment 2 total of 5.44 ± 5.28% trials were discarded.
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54 **Results**

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56 *Systematic shift in the locus of attention relative to the cue after S1_{EYE}-cTBS*
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3 Experiment 1 investigated whether oculoproprioception contributes to locating
4 a non-visual cue relative to a visual target in a cross modal attention task. We
5 predicted that if this is the case, S1_{EYE}-cTBS would shift the locus of attention to
6 reflect the bias in the eye proprioceptive signal. In accord with the prediction, after
7 cTBS over S1_{EYE} we found a cueing error of 0.6°-1.3° towards the midline (to the
8 right in leftward gaze and to the left in rightward gaze) (Figure 4A-B and 6A-B). The
9 cueing error in the post S1_{EYE}-cTBS run was significantly different from the pre-
10 cTBS run at all tested cue locations (paired-samples t-tests: all $p < .03$). cTBS over P3
11 did not significantly change cueing error (Figure 4 C and D, paired-samples t-test: all
12 $p > .32$). The repeated-measures ANOVA of mean cueing error with factors cTBS run
13 (pre vs. post) x stimulation area (S1_{EYE} vs. P3) x gaze direction (left vs. right) showed
14 a significant three-way interaction ($F(1, 9) = 128.87, p < .001$). Both post S1_{EYE}-cTBS
15 values were significantly different from pre S1_{EYE}-cTBS-data (post-hoc pairwise
16 multiple comparison using Tukey's test, both $p < .01$). In comparison, there was no
17 significant change in cueing error after control cTBS over P3 (both $p > .05$).

18
19 A significant interaction was found for gaze direction x cTBS run ($F(1, 9) =$
20 $72.6, p < .001$). This interaction was driven by the post-S1_{EYE}-cTBS effect in different
21 directions for left and right gaze angles (post hoc pairwise multiple comparison using
22 Tukey's test: $p < .01$ for left post-cTBS vs. right post cTBS, all other $p > .05$). None of
23 the other main effects or interactions was significant (all $p > .231$).

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Insert Figure 4 about here

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3 This result was robust across two different methods for calculating the locus of
4 attention. We found the same effect of S1_{EYE}-cTBS when the locus of attention was
5 calculated as the center of mass of the locations that showed a cueing benefit. After
6 cTBS over S1_{EYE} cueing error was 0.4°-1.2° towards center (to the right in leftward
7 gaze and to the left in rightward gaze) (Figure 5A and B). The cueing error in the post
8 S1_{EYE}-cTBS run was significant different from the pre-cTBS run at all tested cue
9 locations (paired-samples t-tests: all $p < .04$). cTBS over P3 did not change cueing
10 error (Figure 5 C and D, paired-samples t-test: all $p > .21$). Repeated-measures
11 ANOVA with factors cTBS run (pre vs. post) x stimulation area (S1_{EYE} vs. P3) x gaze
12 direction (left vs. right) showed a significant three-way interaction ($F(1, 9) = 45.9, p <$
13 $.001$). For leftward gaze, the mean cueing error was $-0.34 \pm 0.3^\circ$ (pre-S1_{EYE}-cTBS)
14 and $-0.1 \pm 0.4^\circ$ (pre-P3-cTBS). For rightward gaze, these values were $0.2 \pm 0.52^\circ$ for
15 pre S1_{EYE}-cTBS, $-0.07 \pm 0.46^\circ$ for pre P3-cTBS. After S1_{EYE}-cTBS the cueing error
16 was $0.71 \pm 0.51^\circ$ in leftward gaze and $-0.78 \pm 0.42^\circ$ in rightward gaze. Both post
17 S1_{EYE}-cTBS values were significantly different from pre S1_{EYE}-cTBS-data (post hoc
18 pairwise multiple comparison using Tukey's test, both $p < .02$).

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Here, as well in the previous analysis, a significant interaction was found for
gaze direction x cTBS run ($F(1,9) = 19.1, p < .001$), driven by the post-S1_{EYE}-cTBS
effect in different directions for left and right gaze angles (post hoc pairwise multiple
comparison using Tukey's test: $p < .01$ for left post-cTBS vs. right post cTBS, all other
 $p > .05$). None of the other main effects and interactions was statistically significant

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3 (all $p > .115$). After P3-cTBS no significant shift in cueing error could be observed
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5 (mean cueing error $-0.33 \pm 0.56^\circ$ for screen left, $0.13 \pm 0.52^\circ$ for screen right, post hoc
6
7 pairwise multiple comparison using Tukey's test: both $p > .05$).
8

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10 Participants' accuracy was close to ceiling. They were correct in $97.85 \pm$
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12 1.73% of the trials. We found no difference in accuracy across conditions. Repeated-
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14 measures ANOVA with factors cTBS run (pre vs. post) x stimulation area (S1_{EYE} vs.
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16 P3) x gaze direction (left vs. right) showed no significant three-way interaction ($F(1,$
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18 $9) = .276, p = .612$). None of the main effects or two-way interactions was significant
19
20 (all $p > .272$).
21

22 23 24 25 *No change in open-loop pointing to visual targets after S1_{EYE}-cTBS*

26
27 Experiment 2 investigated whether S1_{EYE}-cTBS impacts the perceived location
28
29 of visual objects or perceived posture of left hand. If this was the case, one would
30
31 expect an increase in pointing error after S1_{EYE}-cTBS
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34 We did not find a statistically significant increase in pointing error for any
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36 target position, gaze direction or stimulation site (Figure 6, paired-samples t-tests pre-
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38 vs. post-stimulation, all $p > .102$). The mean pointing error over all target locations did
39
40 not change significantly after cTBS (Figure 7 C-D). The repeated-measures ANOVA
41
42 of the pointing error with factors TMS run (pre vs. post) x stimulation area (S1_{EYE} vs.
43
44 P3) x gaze direction (left vs. right) showed no significant three-way interaction ($F(1,$
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46 $9) = 1.33, p > .27$), main effects or two-way interactions (all $p > .112$).
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3 The precision of pointing was not changed either by cTBS either. The
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5 repeated-measures ANOVA with factors TMS run (pre vs. post) x stimulation area
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7 ($S1_{EYE}$ vs. P3) x gaze direction (left vs. right) for the standard deviation of pointing
8
9 error showed no significant three-way interaction ($F(1,9)= 0.98, p> .32$) and no
10
11 significant main effects or two-way interactions (all $p> .181$). For left gaze direction,
12
13 the mean standard deviation (SD) of the pointing error across participants was 0.82
14
15 $\pm 0.44^\circ$ before $S1_{EYE}$ -cTBS and $0.75 \pm 0.50^\circ$ after $S1_{EYE}$ -cTBS. The values for P3-
16
17 cTBS were $1.15 \pm 48^\circ$ (pre-cTBS) and $1.01 \pm 0.35^\circ$ (post c-TBS). For right gaze
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19 direction, participants had SD of $1.83 \pm 0.97^\circ$ before $S1_{EYE}$ -cTBS and $1.36 \pm 0.86^\circ$
20
21 after $S1_{EYE}$ -cTBS. The P3-cTBS values were $1.53 \pm 0.84^\circ$ (pre-cTBS) and $1.49 \pm$
22
23 0.93° (post-cTBS).
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27 Direct comparison between the cueing and pointing error in Experiments 1 and
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29 2 using a repeated-measures ANOVA with factors (1) task (cross-modal attention vs.
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31 pointing), (2) TMS run (pre vs. post), (3) stimulation area ($S1_{EYE}$ vs. P3) and (4) gaze
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33 direction (leftward vs. rightward) showed a statistically significant 4-way interaction
34
35 ($F(1,9)= 13.327, p< .008$). No significant main effects were found (all $p> .105$). All
36
37 significant interactions (task*gaze direction: $F(1,9)= 9.99, p= 0.012$; TMS run*gaze
38
39 direction: $F(1,9)= 13.14, p= 0.006$; task*TMS run*gaze direction: $F(1,9)= 29.67, p<$
40
41 0.001 ; TMS run*stimulation area*gaze direction: $F(1,9)= 27.18, p=0.001$) were
42
43 driven by opposite effect of $S1_{EYE}$ -cTBS for different directions of gaze in the cross-
44
45 modal attention task (post hoc pairwise multiple comparison using Tukey's test: $p<.01$
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47 for left post-cTBS vs. right post cTBS and for left post-cTBS vs. right post-cTBS, all
48
49 other $p> .05$). A post hoc Tukey's test, comparing pre- vs. post-cTBS was only
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51 significant for pre- vs. post- $S1_{EYE}$ -cTBS in the cross-modal attention task for either
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53 gaze direction.
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5 *S1_{EYE}-cTBS in the left hemisphere does not disturb perceived position of the*
6 *ipsilateral, left index finger at rest*

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9 Experiment 3 controlled for an effect of S1_{EYE}-cTBS on felt position of the left index
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finger at rest. If perceived finger position at rest, but not during pointing is disturbed
by cTBS over S1_{EYE}, one would expect an increase in pointing error after S1_{EYE}-cTBS
here.

We found no significant change in pointing error between pre- and post-cTBS over
S1_{EYE} or P3 for any of the 8 tested locations (paired-samples t-tests: all $p > .106$).
Repeated-measures ANOVA of mean pointing errors with factors gaze direction (left
vs. right) x stimulation site (S1_{EYE} vs. P3) x run (pre vs. post) showed neither main
effects nor interactions (all $p > .89$).

The mean pointing error for each participant before and after cTBS over S1_{EYE}
or P3 is shown in panels E-F Figure 7.

Insert Figure 7 about here

Discussion

We found that altering the activity of an oculoproprioceptive area in the human postcentral gyrus is sufficient to divert attention away from behaviorally important cues. Throughout the visual space, cueing error, or the distance between the cue and the locus of attention, matched well in direction and magnitude the bias in perceived eye rotation measured in a previous study (Odoj & Balslev, 2013). This error cannot be explained by a mislocalization of the visual target. Direct comparison between the attention and reaching tasks (Experiment 1 and 2) showed a significant interaction, driven by the larger error for cross-modal attention than for visually-guided reaching. We argue therefore that oculoproprioception is selective for the attention map, as opposed to the visual map for reaching.

Because oculoproprioception was manipulated at cortical level, one could object that the effect of cTBS on attention was merely the result of the disruption of the cortical modules dedicated to this function. This explanation is unlikely. The direction of the cueing error was gaze dependent (leftward in right gaze and rightward in left gaze) and its magnitude at all tested locations matched well the error in perceived eye position (Odoj & Balslev, 2013). *A role of oculoproprioception in coding the locus of attention is compatible with neurophysiological data*

Two neural mechanisms have been proposed to implement a locus of attention that anchors retinotopic representations to the physical location of the visual stimuli. First, populations of gain-field neurons with a retinotopic receptive field scale their activity with the angle of gaze to encode visual location relative to the body and/or the world (Andersen & Mountcastle, 1983; Pouget et al., 2002). A second mechanism is remapping of the retinotopic receptive field to account for eye movements (Duhamel et al., 1992; Mirpour & Bisley, 2012). A role of oculoproprioception in coding the

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3 locus of attention is compatible with both these mechanisms. A signature of the fastest
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5 of the two components of the oculoproprioceptive feedback can be recorded from
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7 somatosensory area 3a already at 5 ms before the end of the saccade (Wang et al.,
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9 2007). This is in line with the time needed for a remapped representation for the locus
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11 of attention to emerge in area LIP, at 8-32 ms after the saccade (Mirpour and Bisley,
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13 2012). Likewise, gain-field neurons show ~150 ms post-saccadic delay in updating
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15 (Xu, Karachi, & Goldberg, 2012), which is compatible with the ~60ms latency of the
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17 slower, tonic (Xu et al., 2011) component of the oculoproprioceptive signal.
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21 *Implications of the current findings for understanding the coupling between*
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23 *the eye and attention*
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26 Although the idea that the eye and attention systems are coupled is not new
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28 (Rizzolatti, Riggio, Dascola, & Umiltá, 1987), the mechanism of this coupling
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30 remains a current topic of debate (Smith & Schenk, 2012; Wright & Ward, 2008).
31
32 We argue here that the attention maps incorporate oculosensory signals, to align
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34 retinotopic representations to physical locations. A role of the oculosensory signals in
35
36 spatial attention is also suggested by observations of a reduced ability to orient
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38 attention to cues in patients suffering from a disease of the extraocular muscles or
39
40 their peripheral innervation (Craighero, Carta, & Fadiga, 2001; Gabay, Henik, &
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42 Gradstein, 2010; Smith, Rorden, & Jackson, 2004). Under the assumption that in
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44 these patients the brain areas that relay the corollary discharge (Sommer & Wurtz,
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46 2008) are normal, such observations can provide insight into the role of the
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48 oculoproprioceptive inflow in spatial attention. Likewise, the allocation of attention
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50 is disrupted at extreme rotations of the eyes (Craighero, Nascimben, & Fadiga, 2004;
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52 Smith, Ball, Ellison, & Schenk, 2010; Smith, Schenk, & Rorden, 2012), a condition
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3 known to cause an abnormal oculoproprioceptive inflow (Ebenholtz, 1974; Paap &
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5 Ebenholtz, 1976).

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7 Smith and Schenk have proposed that the oculomotor signals bias the competition
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9 among sensory inputs, to favor stimuli that are also the end-point of a planned saccade
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11 (Smith & Schenk, 2012). In line with the idea that attention follows the gaze, can an
12
13 alternative explanation of the current results be that oculoproprioception merely
14
15 biases perception to favor visual stimuli nearer the perceived direction of gaze? The
16
17 design of the spatial attention task rules out this explanation. This is because an
18
19 unspecific bias towards perceived direction of gaze would have been identical during
20
21 both conditions, with and without a cue. S1_{EYE} cTBS changed the *difference* in RT
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23 between these two conditions. Thus, cueing error after S1_{EYE} cTBS cannot be
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25 explained by a general bias in spatial attention towards the midline.
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30 *Can the selective role of oculoproprioception in spatial attention be explained*
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32 *by the timing of the underlying neural processing?*
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35 Our result is surprising. We found that participants match the same hand
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37 location with different retinal locations depending on whether the hand acts as an
38
39 attention cue or as an effector for action. These results cannot be explained by
40
41 differences between the attention and pointing task in the timing of the visual target
42
43 onset. Because of the delay in the ascending pathways, oculoproprioception can be
44
45 unreliable for up to 60 ms after an eye movement (Wang et al., 2007; Xu et al., 2011).
46
47 In both tasks participants maintained fixation for 600-750 ms before visual target
48
49 onset. So, it is safe to assume that at target onset, reliable oculoproprioception had
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51 been available. The lack of a detectable effect of the oculoproprioceptive distortion
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53 on visually guided reaching is in line with previous findings. Some studies fail to find
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55 errors in locating visual targets relative to the body when oculoproprioception is
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3 reduced or abnormal (Balslev, Himmelbach, et al., 2012; Lewis et al., 1998), or
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5 calculate a smaller weight for oculoproprioception than for the corollary discharge in
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7 the multimodal estimate of eye position (Bridgeman & Stark, 1991; Gauthier,
8
9 Nommay, & Vercher, 1990).
10

11 We speculate that the reason for the larger weight of oculoproprioceptive
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13 signal from the somatosensory cortex for spatial attention rather than for visually
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15 guided reaching is the timing of the underlying neural processes. If neural processing
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17 necessary to build attention representations exceeds the time interval in which
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19 proprioception is unreliable, and if the neural processing for the visual map does not,
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21 then only the former would incorporate oculoproprioception. In support of this idea,
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23 brain areas that process shape or colour (i.e. mainly dedicated to perceptual
24
25 discrimination) have a longer latency of the visually evoked activity compared with
26
27 brain areas that process luminance or motion (i.e. mainly for action) (Laycock,
28
29 Crewther, & Crewther, 2007; Schmolesky et al., 1998; Schroeder, Mehta, & Givre,
30
31 1998). The longer latency of neural processing for perception vs. action may leave
32
33 more time for computing priority vs. reaching maps. The forward model based on the
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35 corollary discharge provides an early estimate of eye position that is probably
36
37 reasonably accurate, given the predictable environment of the orbits. Therefore, fast
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39 neural processes (i.e. computing visual maps for reaching) are likely to rely on
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41 corollary discharge or alternatively, on oculoproprioceptive input available upstream
42
43 the somatosensory cortex. Subcortical structures that could provide
44
45 oculoproprioceptive signals for visually guided reaching are the superior colliculus,
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47 which in rats is connected to the trigeminal nucleus (Ndiaye, Pinganaud, VanderWerf,
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49 Buisseret-Delmas, & Buisseret, 2000) or the central thalamus that in the monkey
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51 contains neurons sensitive to eye position which discharge after a saccade (Tanaka,
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3 2007). In contrast, neural processes that take longer (i.e. computing the priority map
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5 for perception), may accommodate the delay in the ascending proprioceptive
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7 pathways and benefit from a more robust estimate of eye position by incorporating the
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9 oculoproprioceptive input from the somatosensory cortex.
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17
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21
22 Section of Neuropsychology at the University of Tuebingen
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26 **References**

- 27
28
29 Andersen, R. A., & Mountcastle, B. (1983). The influence of the angle of gaze upon
30 the excitability of the light-sensitive neurons of the posterior parietal cortex.
31 *Journal of Neuroscience*, 3(3), 532–548.
32
33 Andersen, R. A., Snyder, L. H., Bradley, D. C., & Xing, J. (1997). Multimodal
34 representation of space in the posterior parietal cortex and its use in planning
35 movements. *Annu Rev Neurosci*. 1997;20:303-30
36
37
38 Balslev, D., Albert, N. B., & Miall, R. C. (2011). Eye muscle proprioception is
39 represented bilaterally in the sensorimotor cortex. *Human Brain Mapping*, 32(4),
40 624–31.
41
42
43 Balslev, D., Gowen, E., & Miall, R. C. (2011). Decreased visual attention further
44 from the perceived direction of gaze for equidistant retinal targets. *Journal of*
45 *Cognitive Neuroscience*, 23(3), 661–669.
46
47
48 Balslev, D., Himmelbach, M., Karnath, H.-O., Borchers, S., & Odoj, B. (2012). Eye
49 proprioception used for visual localization only in conflict with the oculomotor
50 plan. *Journal of Neuroscience*, 32(25), 8569–8573.
51
52
53 Balslev, D., & Miall, R. C. (2008). Eye position representation in human anterior
54 parietal cortex. *Journal of Neuroscience*, 28, 8968–8972.
55
56 Balslev, D., Newman, W., & Knox, P. C. (2012). Extraocular muscle afferent signals
57 modulate visual attention. *Investigative Ophthalmology & Visual Science*, 53,
58
59
60

1
2
3 7004–7009.
4

- 5 Balslev, D., Odoj, B., & Karnath, H.-O. (2013). Role of somatosensory cortex in
6 spatial attention. *Journal of Neuroscience*, *33*, 18311–18318.
7
- 8 Bridgeman, B., & Stark, L. (1991). Ocular proprioception and efference copy in
9 registering visual direction. *Vision Research*, *31*(11), 1903–13.
10
- 11 Craighero, L., Carta, A., & Fadiga, L. (2001). Peripheral oculomotor palsy affects
12 orienting of visuospatial attention. *Neuroreport*, *12*(15), 3283–6.
13
- 14 Craighero, L., Nascimben, M., & Fadiga, L. (2004). Eye Position Affects Orienting of
15 Visuospatial Attention. *Current Biology*, *14*, 331–333.
16
- 17 Duhamel, J. R., Colby, C. L., & Goldberg, M. E. (1992). The updating of the
18 representation of visual space in parietal cortex by intended eye movements.
19 *Science*, *255*, 90–92.
20
- 21 Durand, J.-B., Camors, D., Trotter, Y., & Celebrini, S. (2012). Privileged visual
22 processing of the straight-ahead direction in humans. *Journal of Vision*, *12*(6),
23 34–34.
24
- 25 Durand, J.-B., Trotter, Y., & Celebrini, S. (2010). Privileged processing of the
26 straight-ahead direction in primate area V1. *Neuron*, *66*(1), 126–37.
27
- 28 Ebenholtz, S. M. (1974). The possible role of eye-muscle potentiation in several
29 forms of prism adaptation. *Perception*, *3*, 477–485.
30
- 31 Eickhoff, S. B., Stephan, K. E., Mohlberg, H., Grefkes, C., Fink, G. R., Amunts, K.,
32 & Zilles, K. (2005). A new SPM toolbox for combining probabilistic
33 cytoarchitectonic maps and functional imaging data. *Neuroimage*, *25*, 1325–
34 1335.
35
- 36 Gabay, S., Henik, A., & Gradstein, L. (2010). Ocular motor ability and covert
37 attention in patients with Duane Retraction Syndrome. *Neuropsychologia*,
38 *48*(10), 3102–9.
39
- 40 Gauthier, G. M., Nommay, D., & Vercher, J. L. (1990). The role of ocular muscle
41 proprioception in visual localization of targets. *Science*, *249*(4964), 58–61.
42
- 43 Geyer, S., Schleicher, A., & Zilles, K. (1999). Areas 3a, 3b, and 1 of human primary
44 somatosensory cortex. *NeuroImage*, *10*(1), 63–83.
45
- 46 Golomb, J. D., Chun, M. M., & Mazer, J. A. (2008). The native coordinate system of
47 spatial attention is retinotopic. *Journal of Neuroscience*, *28*(42), 10654–62.
48
- 49 Golomb, J. D., Nguyen-Phuc, A. Y., Mazer, J. A., McCarthy, G., & Chun, M. M.
50 (2010). Attentional facilitation throughout human visual cortex lingers in
51 retinotopic coordinates after eye movements. *Journal of Neuroscience*, *30*(31),
52 10493–506.
53
54
55
56
57
58
59
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2
3 Gottlieb, J. P., Kusunoki, M., & Goldberg, M. E. (1998). The representation of visual
4 salience in monkey parietal cortex. *Nature*, *391*, 481–4.
5
6 Grubb, J. D., Reed, C. L., Bate, S., Garza, J., & Roberts, R. L. (2008). Walking
7 reveals trunk orientation bias for visual attention. *Perception & Psychophysics*,
8 *70*(4), 688–696.
9
10 Guthrie, B. L., Porter, J. D., & Sparks, D. L. (1983). Corollary discharge provides
11 accurate eye position information to the oculomotor system. *Science*, *221*, 1193–
12 1195.
13
14 Laycock, R., Crewther, S. G., & Crewther, D. P. (2007). A role for the
15 “magnocellular advantage” in visual impairments in neurodevelopmental and
16 psychiatric disorders. *Neuroscience and Biobehavioral Reviews*, *31*(3), 363–76.
17
18 Lewis, R. F., Gaymard, B. M., & Tamargo, R. J. (1998). Efference copy provides the
19 eye position information required for visually guided reaching. *Journal of*
20 *Neurophysiology*, *80*(3), 1605–8. Retrieved from
21
22 Mathôt, S., & Theeuwes, J. (2010). Gradual remapping results in early retinotopic and
23 late spatiotopic inhibition of return. *Psychological Science*, *21*(12), 1793–8.
24
25 Mirpour, K., & Bisley, J. W. (2012). Anticipatory remapping of attentional priority
26 across the entire visual field. *Journal of Neuroscience*, *32*(46), 16449–57.
27
28 Ndiaye, A., Pinganaud, G., VanderWerf, F., Buisseret-Delmas, C., & Buisseret, P.
29 (2000). Connections between the trigeminal mesencephalic nucleus and the
30 superior colliculus in the rat. *Neuroscience Letters*, *294*, 17–20.
31
32 Odoj, B., & Balslev, D. (2013). Visual sensitivity shifts with perceived eye position.
33 *Journal of Cognitive Neuroscience*, *25*, 1180–1189.
34
35 Paap, K. R., & Ebenholtz, M. (1976). Perceptual consequences of potentiation in the
36 extraocular muscles: an alternative explanation for adaptation to wedge prisms.
37 *J.Exp.Psychol.Hum.Percept.Perform.*, *2*, 457–468.
38
39 Pouget, A., Deneve, S., & Duhamel, J. R. (2002). A computational perspective on the
40 neural basis of multisensory spatial representations. *Nature Reviews*
41 *Neuroscience*, *3*(9), 741–747.
42
43 Reed, C. L., Grubb, J. D., & Steele, C. (2006). Hands Up: Attentional Prioritization of
44 Space Near the Hand. *Journal of Experimental Psychology: Human Perception*
45 *and Performance*, *32*(1), 166–177.
46
47 Rizzolatti, G., Riggio, L., Dascola, I., & Umiltá, C. (1987). Reorienting attention
48 across the horizontal and vertical meridians: evidence in favor of a premotor
49 theory of attention. *Neuropsychologia*, *25*(1A), 31–40.
50
51 Schmolesky, M. T., Wang, Y., Hanes, D. P., Thompson, K. G., Leutgeb, S., Schall, J.

- 1
2
3 D., & Leventhal, A. G. (1998). Signal timing across the macaque visual system.
4 *Journal of Neurophysiology*, 79(6), 3272–8. Schroeder, C. E., Mehta, A. D., &
5 Givre, S. J. (1998). A spatiotemporal profile of visual system activation revealed
6 by current source density analysis in the awake macaque. *Cerebral Cortex*, 8(7),
7 575–92.
8
9
10 Sherrington, C. S. (1918). Observations on the sensual role of the proprioceptive
11 nerve-supply of the extrinsic ocular muscles. *Brain*, 41(3-4), 332–343.
12
13 Smith, D. T., Ball, K., Ellison, A., & Schenk, T. (2010). Deficits of reflexive attention
14 induced by abduction of the eye. *Neuropsychologia*, 48(5), 1269–76.
15
16 Smith, D. T., Rorden, C., & Jackson, S. R. (2004). Exogenous orienting of attention
17 depends upon the ability to execute eye movements. *Curr Biol.*, 14, 792–795.
18
19 Smith, D. T., & Schenk, T. (2012). The Premotor theory of attention: time to move
20 on? *Neuropsychologia*, 50(6), 1104–14.
21
22 Smith, D. T., & Schenk, T. (2012). The Premotor theory of attention: Time to move
23 on? *Neuropsychologia*, 50, 1104–1114.
24
25 Smith, D. T., Schenk, T., & Rorden, C. (2012). Saccade preparation is required for
26 exogenous attention but not endogenous attention or IOR. *Journal of*
27 *Experimental Psychology. Human Perception and Performance*, 38(6), 1438–47.
28
29 Sommer, M. A., & Wurtz, R. H. (2008). Brain circuits for the internal monitoring of
30 movements. *Annual Review of Neuroscience*, 31, 317–38.
31
32 Steinbach, M. J. (1986). Inflow as a long-term calibrator of eye position in humans.
33 *Acta Psychol.*, 63, 297–306.
34
35 Talsma, D., White, B. J., Mathôt, S., Munoz, D. P., & Theeuwes, J. (2013). A
36 Retinotopic Attentional Trace after Saccadic Eye Movements : Evidence from
37 Event-related Potentials. *Journal of Cognitive Neuroscience*, 25(9), 1563–1577.
38
39 Tanaka, M. (2007). Spatiotemporal properties of eye position signals in the
40 primate central thalamus. *Cerebral Cortex*, 17(7), 1504–15.
41
42
43
44 von Helmholtz, H. (1925). *Helmholtz's Treatise on Physiological Optics. Vol 3.* (J. P.
45 C. Southhall, Ed.). New York: Optical Society of America, Electronic edition
46 (2001): University of Pennsylvania. Wang, X., Zhang, M., Cohen, I. S., &
47 Goldberg, M. E. (2007). The proprioceptive representation of eye position in
48 monkey primary somatosensory cortex. *Nature Neuroscience*, 10(5), 640–646.
49
50 Wright, R. D., & Ward, L. M. (2008). *Orienting of attention*. Oxford University
51 Press.
52
53
54 Wurtz, R. H. (2008). Neuronal mechanisms of visual stability. *Vision Research*, 48,
55 2070–89. Xu, B. Y., Karachi, C., & Goldberg, M. E. (2012). The postsaccadic
56 unreliability of gain fields renders it unlikely that the motor system can use them
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to calculate target position in space. *Neuron*, 76(6), 1201–9. Xu, Y., Wang, X., Peck, C., & Goldberg, M. E. (2011). The time course of the tonic oculomotor proprioceptive signal in area 3a of somatosensory cortex. *Journal of Neurophysiology*, 106(1), 71–7.

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10 **Figure 1. Setup and task for the cross-modal attention experiment. A.** In right eye
11 vision, participants fixated at $+19^\circ$ (Experiment 1A, rightward gaze) or -19°
12 (Experiment 1B, leftward gaze) from the center of the right orbit. A somatosensory
13 cue (the participants' left index finger, hidden from view) was positioned at 1 of 4
14 possible locations: $+8^\circ$, $+18^\circ$, $+20^\circ$ or $+30^\circ$ (Experiment 1A) or -8° , -18° , -20° or -
15 30° (Experiment 1B) from orbit midline (here, Experiment 1B: fixation at -19° , cue at
16 -30° from orbit midline). **B.** A target letter, 'A' or 'H', was presented for 100 ms at 1 of
17 7 possible locations, at -3, -2, -1, 0, +1, +2 and +3 degrees horizontally from the cue.
18 Participants named the letter as fast and correct as possible. Voice reaction time and
19 accuracy were recorded. The solid line shows eye position at fixation. The dotted line
20 shows perceived eye position after $S1_{EYE}$ -cTBS according to (Odoj & Balslev, 2013).
21 We predicted a shift of the locus of attention congruent to the shift in perceived gaze
22 towards the center of the orbit for all cue locations.
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41 **Figure 2. Cueing error in one example participant with a somatosensory cue at -**
42 **30° from orbit midline, before and after $S1_{EYE}$ -cTBS.** Before cTBS over $S1_{EYE}$
43 (●), the largest decrease in reaction time in the presence vs. in the absence of the cue
44 occurred for the target that appeared at the same location as the cue (black arrow,
45 cueing error= 0°). After $S1_{EYE}$ -cTBS (○) the largest benefit of the cue was observed
46 for the target that appeared at 1° towards the midline (white arrow)
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Figure 3: Setup and task for the visual open-loop pointing experiment. A.

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3 Participants fixated at +19° (Experiment 2A) or -19° (Experiment 2B) from the center
4 of the orbit, while a position marker was attached to their left index finger (here:
5 fixation at -19°). **B.** A target (letter 'X') was presented for 100 ms at 1 of 4 possible
6 positions: +8°, +18°, +20°, +30° from orbit midline (Experiment 2A) or -8°, -18°, -
7 20°, -30° from orbit midline (Experiment 2B). After target presentation, participants
8 closed their eyes and pointed to the location where the target appeared. Finger
9 location was recorded, and then the finger was passively moved back to the resting
10 position. The solid line shows eye position at fixation. The dotted line shows
11 perceived gaze direction after S1_{EYE}-cTBS according to (Odoj & Balslev, 2013).
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Figure 4. Systematic shift in the locus of attention after S1_{EYE}-cTBS. The locus of
25 attention was defined as the location with the largest benefit of the cue. In leftward
26 gaze, there was a rightward cueing error after S1_{EYE}-cTBS (**A**) at all cue locations.
27 This error was specific to S1_{EYE}-cTBS and did not occur after the stimulation of the
28 control site P3 (**C**). Likewise, in rightward gaze, there was a leftward cueing error at
29 all cue locations after S1_{EYE}-cTBS (**B**) but not after P3-cTBS (**D**). All values with
30 standard error of mean. * denotes $p < .05$, ** denotes $p < .01$, paired-samples t-test.
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Figure 5. Systematic shift in the locus of attention after S1_{EYE}-cTBS. The locus of
43 attention was defined as the center of mass of all locations that showed a benefit of
44 the cue. In leftward gaze, there was a rightward cueing error after S1_{EYE}-cTBS (**A**) at
45 all cue locations. This error was specific to S1_{EYE}-cTBS and did not occur after the
46 stimulation of the control site P3 (**C**). Likewise, in rightward gaze, there was a
47 leftward cueing error at all cue locations after S1_{EYE}-cTBS (**B**) but not after P3-cTBS
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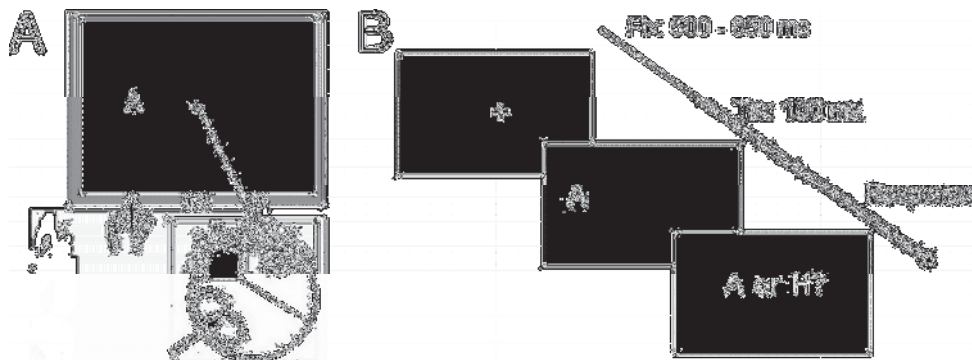
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3 (D). All values with standard error of mean. * denotes $p < .05$, ** denotes $p < .01$,
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5 ***denotes $p < .001$ in paired-samples t-test.
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10 **Figure 6. No shift in visual pointing for any cueing position after S1_{EYE}- or P3-**
11 **cTBS.** In leftward gaze, there was a rightward pointing error after S1_{EYE}-cTBS (A).
12 This error was specific to S1_{EYE}-cTBS and did not occur after the stimulation of the
13 control site P3 (C). In rightward gaze, there was a leftward pointing error only after
14 S1_{EYE}-cTBS (B) but not after P3-cTBS (D). All values with standard error of mean. *
15 denotes $p < .05$, ** denotes $p < .01$ in paired-samples t-test.
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25 **Figure 7. The effect of S1_{EYE}-cTBS is specific for coding the locus of attention.**

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27 Upper row shows the mean cueing error in the cross-modal attention task for leftward
28 (A) and rightward (B) gaze. The middle row shows the mean error for open-loop
29 pointing to visual targets (C, D), the lower row shows the pointing error to
30 somatosensory targets (E, F). In the left column data for left gaze direction is shown,
31 the right column shows data for right gaze direction. Filled circles (●) show pre-
32 cTBS-data, empty circles (○) show post-cTBS-data. Only changes in cueing error
33 after S1_{EYE}-cTBS were significant. All values with one standard deviation. ** denotes
34 $p < .01$ in post-hoc multiple comparison using Tukey's test.
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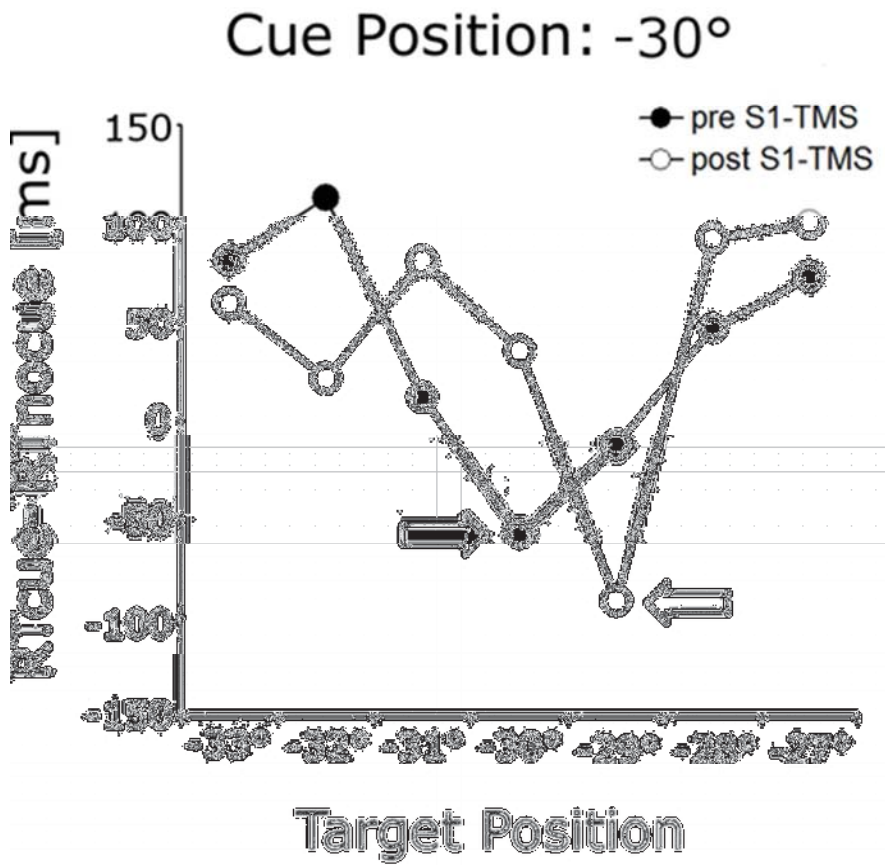
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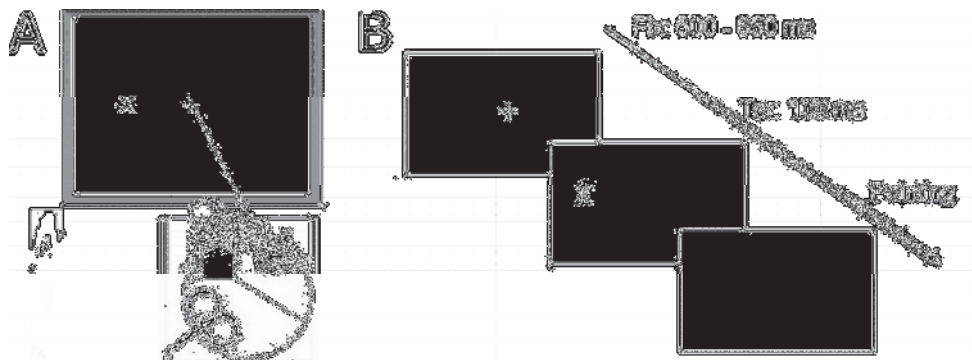
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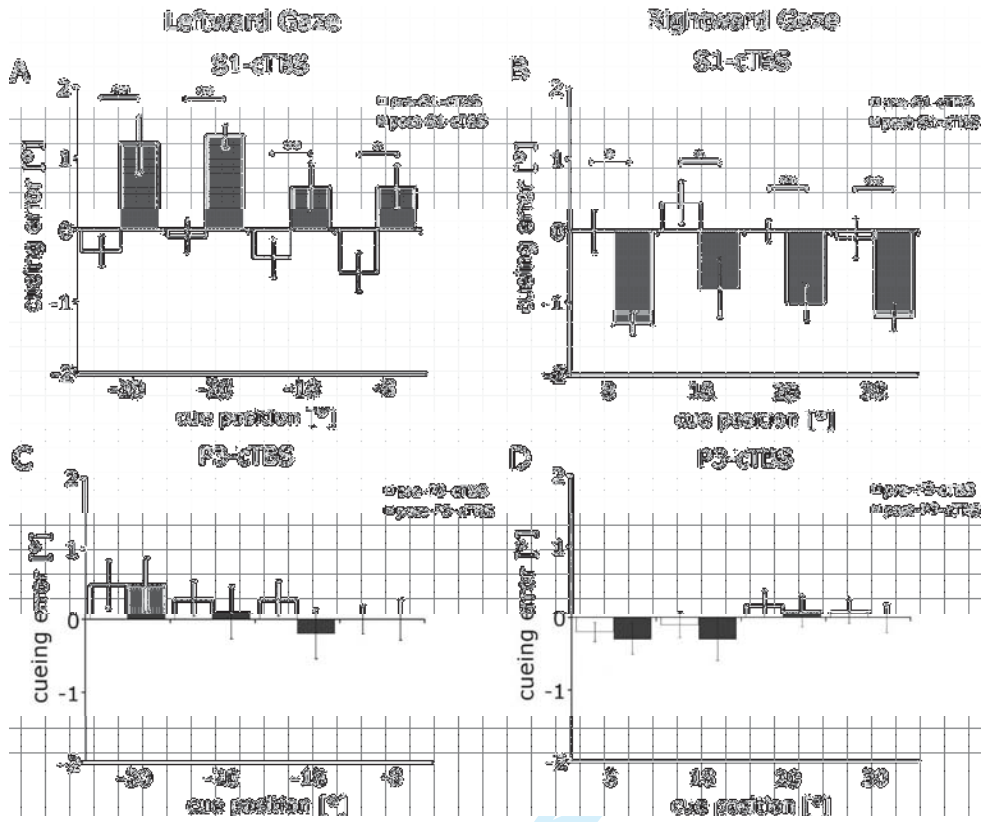
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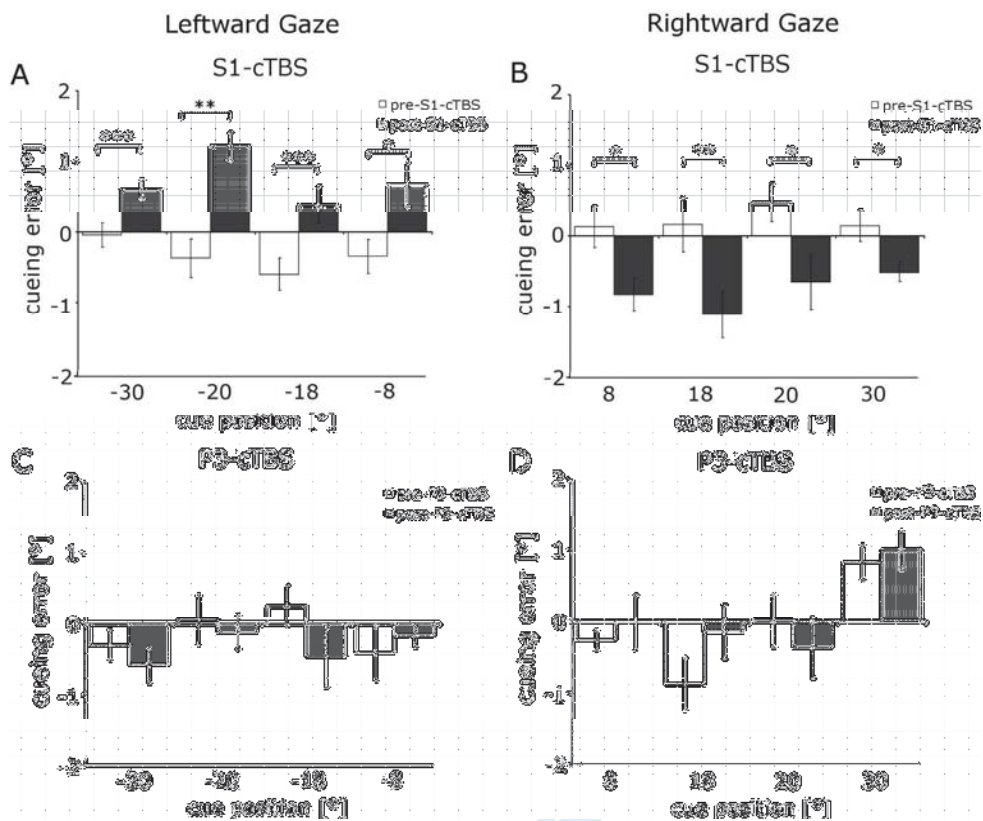
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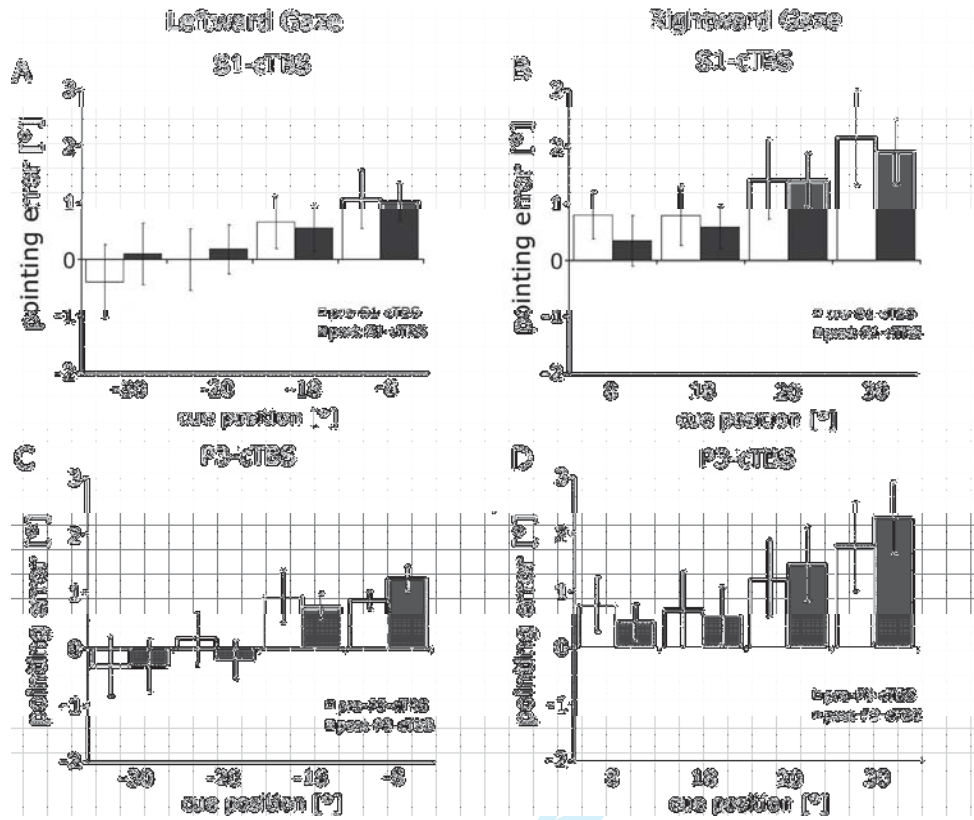
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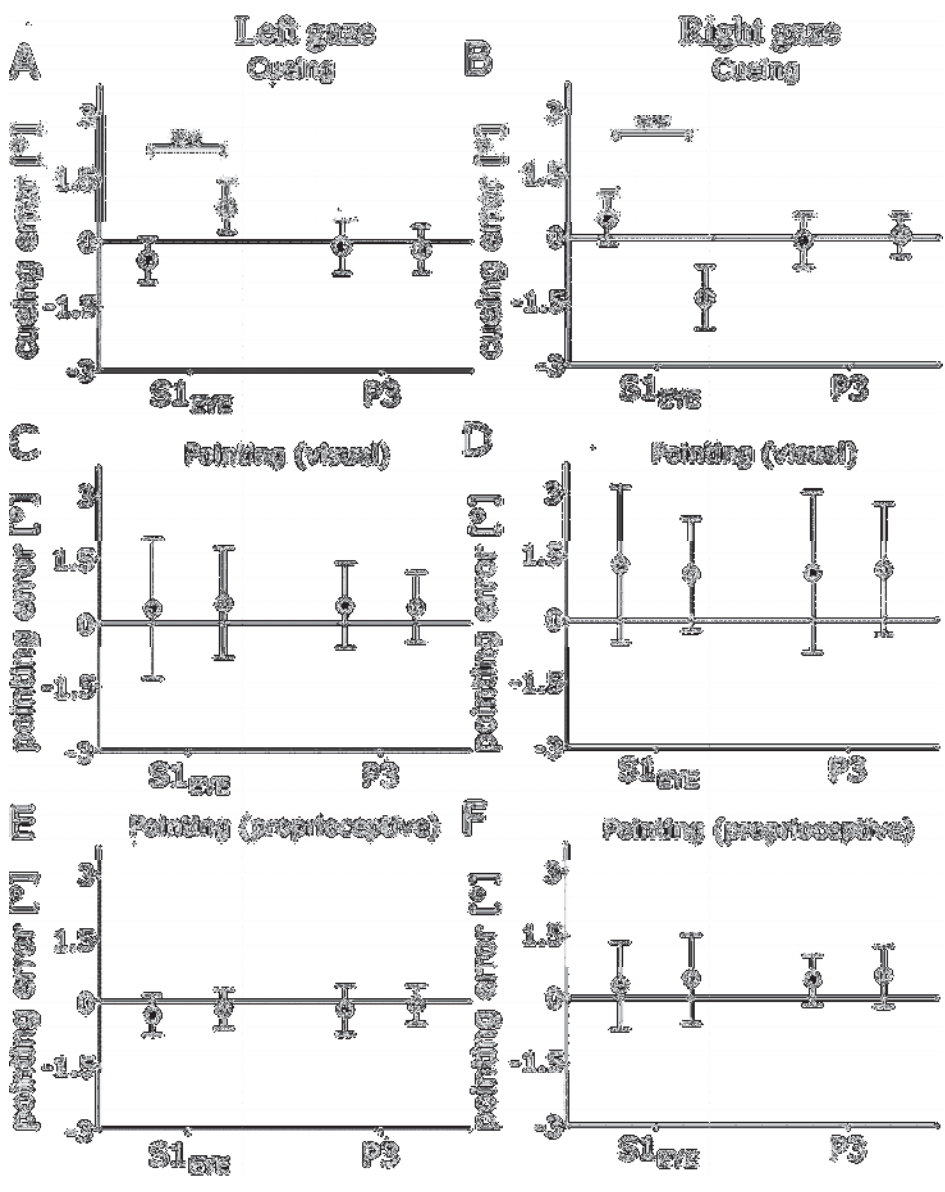
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