Eye Muscle Proprioception Is Represented Bilaterally in the Sensorimotor Cortex

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Abstract: The cortical representation of eye position is still uncertain. In the monkey a propriocep- tive representation of the extraocular muscles (EOM) of an eye were recently found within the con- tralateral central sulcus. In humans, we have previously shown a change in the perceived position of the right eye after a virtual lesion with rTMS over the left somatosensory area. However, it is possible that the proprioceptive representation of the EOM extends to other brain sites, which were not examined in these previous studies. The aim of this fMRI study was to sample the whole brain to identify the proprioceptive representation for the left and the right eye separately. Data were acquired while passive eye movement was used to stimulate EOM proprioceptors in the absence of a motor command. We also controlled for the tactile stimulation of the eyelid by removing from the analysis voxels activated by eyelid touch alone. For either eye, the brain area commonly acti- vated by passive and active eye movement was located bilaterally in the somatosensory area extending into the motor and premotor cytoarchitectonic areas. We suggest this is where EOM pro- prioception is processed. The bilateral representation for either eye contrasts with the contralateral representation of hand proprioception. We suggest that the proprioceptive representation of the two eyes next to each other in either somatosensory cortex and extending into the premotor cortex reflects the integrative nature of the eye position sense, which combines proprioceptive information across the two eyes with the efference copy of the oculomotor command. *Hum Brain Mapp 00:000– 000, 2010.*   © **2010 Wiley-Liss, Inc.**

Key words: fMRI; cortical; eye position; oculomotor; proprioceptive; somatosensory

INTRODUCTION

The human extraocular muscles (EOM) have proprio- ceptive receptors, similar to skeletal muscle spindles [Donaldson, 2000] whose signals, along with the efference copy of the motor command, are used to compute eye position [Allin et al., 1996; Gauthier et al., 1990; Han and Lennerstrand, 1999]. Finding the cortical projection of the proprioceptive signal has been the focus of current research. In the monkey, a proprioceptive representation of the EOM was recently found within the central sulcus contralateral to the eye [Wang et al., 2007]. In humans, we have previously shown a change in the perceived position

of the right eye after a virtual lesion with rTMS over the left somatosensory area [Balslev and Miall, 2008].

However, both these previous studies specifically tested the role of the contralateral somatosensory cortex, the most likely area to receive this signal. It may be the case that the somatosensory representation of the eye deviates from this well known pattern. First, eye position modulates the activity at premotor, parietal, and occipital sites in both monkeys [Andersen and Mountcastle, 1983; Boussaoud et al., 1998; Galletti and Battaglini, 1989] and humans [Baker et al., 1999; De Souza et al., 2000, 2002]. Because eye proprioception conveys eye position, it may be possible that the proprioceptive signal reaches these areas too. Second, unlike for other distal effectors, the sense of eye position combines proprioceptive information across the two eyes. For instance when one eye is passively deviated in one direction by peripheral manipulation, the other eye is felt as being deviated in that direction too [Gauthier et al., 1990]. This integrated sense of position argues for anatomical proximity of the proprioceptive projection from the two eyes in the central nervous system. In the frontal eye fields, an area that transforms visual input into oculomotor commands [Schall, 2002], each eye is represented on both hemispheres [Blanke and Seeck, 2003; Rafal, 2006]. In analogy, it may be possible that the somatosensory representation of the EOM is similarly organized.

The aim of this study was to identify the EOM proprioceptive representation in the human brain with fMRI. Active eye movement would be expected to activate the EOM proprioceptors but would also invoke a motor command. Hence we also used passive movement to stimulate the proprioceptors in the absence of an ocular motor command. Without visual feedback, pressing one eye produces a passive rotation of the eye in the absence of movement of the other eye [Ilg et al., 1989], which there is no oculomotor command in response to the passive deviation of one eye. The participants briefly pressed (<1 s) their eye with their index finger from the contralateral hand. To control for brain activity evoked by the movement of the finger, we added a voluntary eye movement condition. This condition stimulates the EOM proprioceptive receptors, but involves no finger movement. The activity common to both active and passive eye movement would include activity related to the EOM proprioceptive component, without activity related to finger movement. Tactile stimulation on the outer eyelid occurs during passive eye movement and some tactile stimulation on the inner eyelid occurs both during active and passive movement. To remove this tactile component, we added a control condition where the participants gently touched their eyelid with their index finger – without inducing movement of the eyeball. We used a very liberal threshold ($P > 0.05$ uncorrected) to identify the voxels activated by a mere touch on the eyelid. These voxels were removed from the analysis to ensure that our results do not involve the tactile component. Thus, we assumed that the brain areas where EOM proprioception projects to would activate during both active and passive eye movement, but not during tactile stimulation of the eyelid alone.

METHODS

Participants

Eighteen healthy, right-handed adults (12 female, age median 21, range 18–53) gave written informed consent to participate in this study and received financial compensation for their time. The study was approved by the School of Psychology Ethics Committee at the University of Birmingham.

Task

Experiment 1: Eye position

Each participant completed six runs (three runs for each eye). They kept their eyes closed throughout the experiment. One hand rested on top of the head coil so that their index finger could easily reach the outer canthus of the eyelid contralateral to the hand. There were four different types of trials: (a) *passive* (the participant briefly pushed the eye medially with their index finger, which touched the eyelid at the outer canthus. The push was as brief as possible lasting less than 1 s.); (b) *touch* (the participant touched the eyelid at the same location, without moving the eyeball); (c) *active* (the participant shifted their gaze—with eyes closed—to one side then back to the central position); and (d) *rest*.

Trials of each type were grouped in 25 s blocks. Each block began with a verbal instruction (4.8 s duration). Within each block, a 100 ms tone cued the start of each trial. The time interval between the onsets of two consecutive trials was chosen randomly from a normal distribution with a mean of 2 s and standard deviation of 0.5 s (range 1.34–2.82 s). The median number of trials in each block was 10 (range 9–11). The participants performed each block type four times within each 400-s run. Block order was counterbalanced across runs and subjects.

Before the experiment, participants practiced pushing their eyeball during normal binocular vision, and increased the force until they produced double vision. An eye press of a strength that produces double vision should be sufficient to passively displace the eyeball in the absence of visual feedback.

When the right eye was tested, participants pushed or touched their right eyelid using their left index finger or shifted their gaze to the left then back to center. For the left eye, they did the opposite. Order of exposure was counterbalanced across participants.

The participants were asked to demonstrate all tasks outside the scanner while lying on the scanner bed with the head coil on to ensure participants understood and were able to perform these tasks.

Experiment 2: Finger tapping

To locate the EOM proprioceptive representation relative to the hand area, participants completed two runs of index finger tapping alternating with rest. The participants' arms were relaxed by their side supported by cushions. There were two types of trials: (a) *tap* (the participant tapped with their left index finger) and (b) *rest*. The start of each trial was signaled by an auditory cue. The trials were grouped in blocks of 25 s each and presented alternately. The order of condition presentation was randomized across subjects. The two hands were tested in separate runs in counterbalanced order.

Data Acquisition

Gradient-echo echo-planar images were acquired with a 3-T Philips Achieva scanner with TR = 3 s/volume, TE = 0.035 s, FOV = 240 mm × 147 mm × 240 mm (in antero-posterior, inferior to superior, right to left direction, respectively) and voxel size = 2.5 mm × 2.5 mm × 3 mm. Forty-nine horizontal slices of 3 mm thickness covering the entire brain including the cerebellum were acquired from the bottom to the top of the brain. In addition, whole brain T1-weighted anatomical scans were collected with 1 mm × 1 mm × 2 mm resolution.

Statistical Analysis

Data were analyzed with SPM5 (http://www.fil.ion. ucl.ac.uk/spm/software/spm5). The images were realigned, slice-timing corrected, spatially normalized to MNI152-template (ICBM) and smoothed with an 8 mm FWHM filter. The design matrix for single subject analyses included three regressors (passive, touch, and active) in Experiment 1 or one regressor (finger tapping) in Experiment 2. The timing of these events was calculated from the vector of onset for the pacing tone by adding 0.4 s to approximate the participant's reaction time. The design matrix also included a regressor for the onset of the sound signal regardless of trial type. All events were modeled by convolving the event vectors with the hemodynamic response function. To account for head motion, the six parameters from the realignment transformations (three translations, three rotations) were added to the design matrix. The cut-off frequency for high-pass filtering was 1/128 s.

For Experiment 1, to identify areas that receive EOM proprioceptive input we used the conjunction (*passive-rest*) AND (*active-rest*) masked exclusively with the contrast *touch-rest*. This was done in a random effects analysis using the conjunction null hypothesis [Friston et al., 2005]. The threshold for the mask *touch-rest* was P = 0.05. We chose this very liberal treshold for this exclusive mask to remove from the conjunction any activity related to tactile stimulation of the eyelid. The threshold for the conjunction analysis was P = 0.05, corrected for multiple comparisons. We report both suprathreshold single voxels with a voxel

TABLE I. Eye muscle proprioceptive representation

Area	Voxel MNI coordinate			Probabilistic atlas location (%) Brodmann Area				
	x	y	z	3b	3a	4p	4a	6
Right eye								
L SMC	−36	−16	40	10	20	50	0	0
R SMC	36	−14	38	10	40	50	0	0
	44	−6	44	0	0	0	10	30
Left eye								
L SMC	−38	−12	42	10	0	20	20	0

Note: The table shows the supra-threshold peak voxels for the conjunction between active and passive eye movement [(active − rest) AND (passive − rest)] after masking out the voxels showing activity during (touch − rest). The threshold was set at voxel *P*-value = 0.05, corrected for multiple comparison using FWE. The threshold of the exclusive mask was 0.05 uncorrected for multiple comparisons. (SMC, sensorimotor cortex; L, left; R, right).

P-value <0.05, corrected for multiple comparisons using FWE and suprathreshold clusters of contiguous voxels with *t* > 2.75, where the cluster *P*-value <0.05, corrected for multiple comparisons.

In addition, the contrast *active-rest* was used to identify the brain areas activated during active eye movement for comparison of their anatomical location with that of the EOM proprioceptive representation. Lastly, to ensure that the EOM proprioception representation was not polluted by the finger movements that occurred during Experiment 1, the sensorimotor hand area was identified using the subtraction *tap-rest*. For anatomical localization, MNI coordinates of these voxels were found in the probabilistic stereotaxic cytoarchitectonic atlas of the Anatomy Toolbox v1.5 [Eickhoff et al., 2005].

RESULTS

For the right eye, the conjuction analysis identified three suprathreshold voxels (voxel *P* > 0.05 FEW corrected) located symmetrically in the sensorimotor cortex of both hemispheres (Table I and Fig. 1a, top pannel) and one suprathreshold cluster in the ipsilateral (right) hemisphere (561 contiguous voxels, 4.4 cm^3, voxel *P* > 0.05 corrected for multiple comparisons) (Fig. 1b, top pannel). For the left eye, the conjuction identified one suprathreshold voxel located in the ipsilateral sensorimotor cortex (Table I and Fig. 1a, bottom pannel) and one suprathreshold cluster (409 contiguous voxels, 3.2 cm^3) located in the contralateral (right) sensorimotor cortex (Fig. 1b, bottom pannel). No other significant voxels or clusters were found. Thus, for both eyes, the whole brain analysis returned a bilateral pattern of activation in the somatosensory and motor cortices.

The probable location for the peak activated voxels for the eye proprioceptive representation was in areas 4p, 3a,
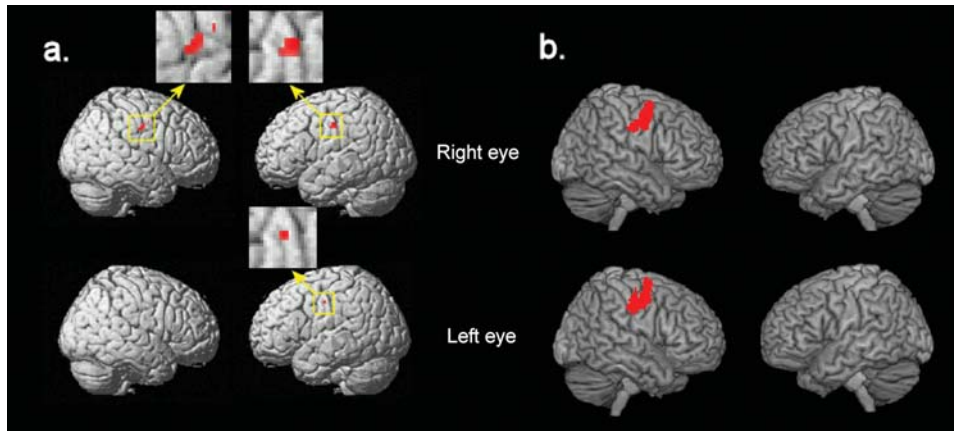
Figure 1.

Eye muscle proprioceptive representation. (**a**) Suprathreshold voxels ($P = 0.05$ corrected for multiple comparisons using FWE and (**b**) suprathreshold clusters ($P = 0.05$ corrected for multiple comparisons). The activations are defined by the conjunction between active and passive eye movement [(active-rest) AND (passive-rest)] after removing the voxels activated by tactile stimulation of the eyelid (touch-rest). The threshold of the exclusive mask (touch-rest) was 0.05 uncorrected. Top panel: right eye proprioceptive representation, bottom pannel: left eye proprioceptive representation. For localization purposes the functional map is overlaid on a single-subject structural MR-template (SPM5).

and 3a (Table I). At these locations the BOLD signal increased in the conditions that involved active and passive movement of the eye and showed no change or even a decrease in activity during tactile stimulation of the eyelid (Fig. 2).

Voluntary eye movement (active-rest) activated areas in the premotor, supplementary motor, posterior parietal cortex, and the cerebellum (Fig. 3), in line with previous reports [Corbetta et al., 1998; Grosbras et al., 2005]. The Brodmann area location of the voxels in the precentral and postcentral gyri are reported in Table II. As expected, the coordinates of the peak activations during active eye movement were anterior of the peak activations of the eye proprioceptive representation, with some overlap. Although the group level cluster found during active eye movement had local maxima within BA 3a, 3b, 4a, 4b, and 6 (Table II) similar to the proprioceptive representation of EOM, the distribution of this activity differed between the two contrasts. For the active eye movement the activity was strongly biased toward motor/premotor cytoarchitectonic areas, whereas for eye proprioception, the activity was distributed more equally across the central sulcus. Thus, three of four peak voxels for the eye proprioceptive representation had some probability of location within a somatosensory area, whereas for active eye movement only one of six suprathreshold voxels could have fallen within a somatosensory cytoarchitectonic area (Table II).

For Experiment 2, finger tapping activated areas in the frontal and parietal lobes and the cerebellum in line with previous reports [Cramer et al., 1999]. For the purpose of this study, we focused on the voxels in the precentral and postcentral gyri. Right index finger tapping activated the contralateral precentral/postcentral gyrus, whereas for the left index finger the activation was bilateral, albeit with the largest cluster in the contralateral hemisphere (Table III). All but one of these local maxima fell within premotor and motor cytoarchitectonic areas and had zero probability of being located within a somatosensory cytoarchitectonic area.

DISCUSSION

This fMRI study identified a proprioceptive representation of the eye muscles as bilateral, in the somatosensory cortex and extending into the motor cortex. This pattern of activation was common for both eyes. We suggest that this is the cortical site where EOM proprioception is relayed.

The suprathreshold voxels were located within both the postcentral and precentral gyri. It is unlikely that this anatomical location in the motor cortex reflects a contamination due to a motor command to EOM for three reasons. First, eye position recordings using a very sensitive technique (scleral search coils) have shown that in the absence of visual feedback, pressing the eye produces rotation of that eye alone while the contralateral eye does not move [Ilg et al., 1989]. This suggests that passive eye movement evokes no reactive ocular motor command. Second, the clusters of activation in our study were located posterior to the putative location of the frontal eye fields, as identified with meta-analytical techniques across a large number of functional imaging studies [Grosbras et al., 2005; Nielsen and Hansen, 2002]. Third, we did not find any associated activation in the posterior parietal lobes, which is typically associated with active eye movement or shifting attention [Grosbras et al., 2005]. This suggests that the
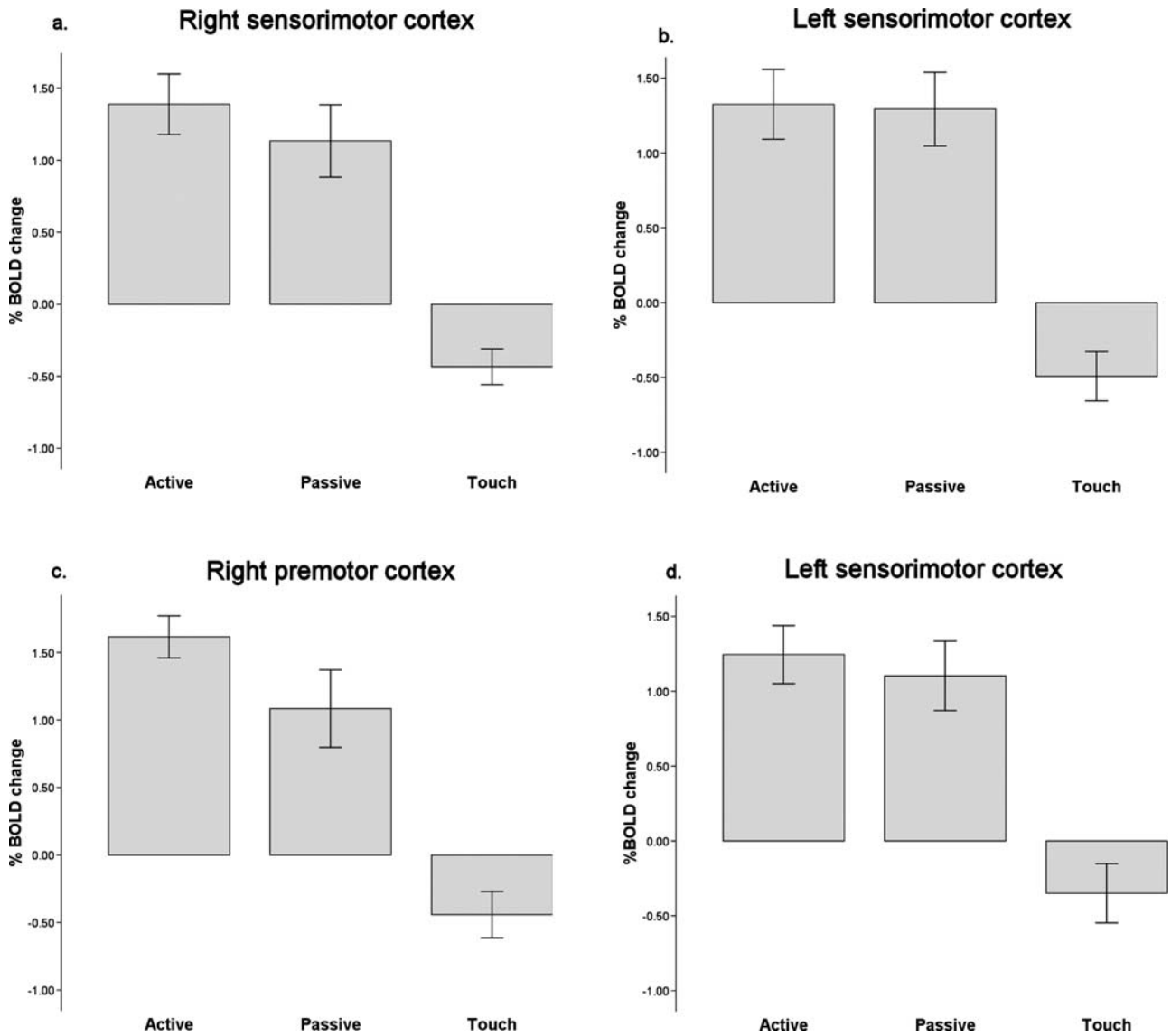
Figure 2.

Activity change across conditions at the peak activated voxels. For the right eye proprioceptive representation these voxels were located in (**a**) the ipsilateral (right) sensorimotor cortex $(x, y, z) = (36, -14, 38)$, (**b**) the contralateral (left) sensorimotor cortex $(x, y, z) = (-36, -16, 40)$, and (**c**) premotor cortex $(x, y, z) = (44, -6, 44)$. For the left eye proprioceptive representation the only suprathreshold voxel was located in (**d**) the ipsilateral (left) sensorimotor cortex $(x, y, z) = (-38, -12, 42)$. The bars show percent BOLD change in the active, passive, and touch conditions relative to mean brain activity during the rest condition. The error bars show one standard error.

regions identified in this study differ from those actively controlling eye movements or shifts in spatial attention.

Similarly, it is unlikely that the index finger movement used to push or touch the eye in the passive and touch trials contaminated the representation of eye proprioception. The eye proprioceptive representation was identified using the conjunction (*passive-rest*) AND (*active-rest*). The conjunction identifies areas that are activated during both contrasts. There was no finger movement in the active condition and therefore it is unlikely that this contrast, and therefore the conjunction, would be driven by finger movement.

Finally, the liberal threshold of the exclusive mask (touch-rest) we used rules out a contamination from tactile stimulation of the eyelid and activation due to finger movement. BOLD activity plots confirmed that at all suprathreshold voxels activity increased during active and passive eye movement, whereas during tactile stimulation
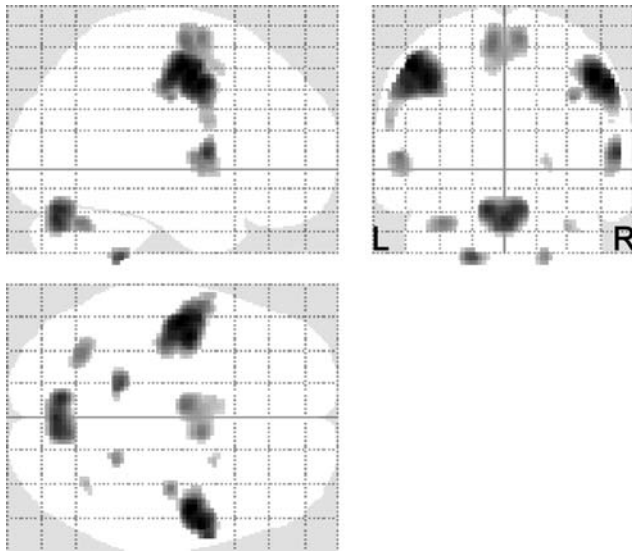
Figure 3.

Eye muscle proprioceptive and motor representation during active eye movements The statistical parametric map was defined by the contrast (active-rest) and thresholded at $P = 0.05$ corrected for multiple comparisons using FWE. Glass brain representation in three orthogonal projections (left side of the brain is shown to the left).

of the eyelid the activity was either unchanged or even decreased relative to mean brain activity. However, because of the very low threshold of the exclusive mask for the conjunction analysis, the statistically significant voxels that survived the masking may be an underestimation of the true spatial extent of the eye proprioceptive representation. For instance, if somatosensory areas that receive proprioceptive input partially overlap with brain

TABLE II. Eye muscle proprloceptlve and motor representation in the sensorimotor cortex

Area	Voxel MNI coordinate			Probabilistic atlas location (%) Brodmann Area			
	x	y	z	1–3	4p	4a	6
LSMC							
	−46	−8	52	0	0	20	90
	−50	−4	44	0	0	0	60
	−40	−4	46	0	0	10	20
RSMC							
	46	−4	46	0	0	0	40
	36	−14	36	60	40	0	0
	54	0	42	0	0	0	60

Note: The table shows a summary of the peak voxels (voxel $P = 0.05$, corrected for multiple comparisons using FWE) defined by the subtraction (active – rest) for Experiment 1. The table shows only the clusters of voxels in the somatosensory and motor cortex. The notation conventions are identical with those in Table I.

TABLE III. Hand proprioceptive and motor representation in the sensorimotor cortex

Area	Voxel MNI Coordinate			Probabilistic location (%) Brodmann Area			
	x	y	z	1–3	4p	4a	6
Right hand LSMC							
	−46	−6	56	0	0	0	80
	−34	−14	52	0	10	40	40
	−36	−24	54	30	40	30	0
	−52	−2	44	0	0	0	50
	−32	−18	68	0	0	0	50
	−28	−18	70	0	0	10	80
Left hand R SMC							
	38	−16	52	0	10	70	50
	38	−26	58	0	30	70	20
	38	0	60	0	0	0	0
	30	−16	70	0	0	0	60
L SMC							
	−40	−4	40	0	10	10	0
	−44	−4	42	0	0	10	30
	−40	0	48	0	0	0	30
	−40	0	58	0	0	0	30

Note: The table shows the peak voxels ($P = 0.05$ corrected for multiple comparisons) defined by the subtraction (tap – rest) for Experiment 2. For the purposes of this study, the table shows only the voxels in the somatosensory and motor cortex. The notation conventions are identical with those in Table I.

areas that receive tactile input from the eyelid, common areas would be masked out by the current analysis.

Although the cytoarchitectonic areas for the peak voxels in the eye proprioceptive representation were similar to those for the sensorimotor representations for eye/hand movement (Tables I–III), the distribution of probabilities among these cytoarchitectonic areas differed between the eye proprioceptive and the eye/hand sensorimotor representation. Thus, activation peaks with some probability for a somatosensory area label were much more frequent in the eye proprioceptive representation (three of four statistically significant single voxels for both eyes) than in the eye or hand representation (one of six or one of 14, respectively). This also argues for the difference between these two sets of functional maps and is compatible with the idea that the EOM proprioceptive representation occupies the most posterior part of the EOM sensorimotor representation.

One of the suprathreshold voxels of the proprioceptive representation for the right eye was located in the premotor/motor cortex of the right hemisphere $(x, y, z) = (44, −6, 44)$ (Table I, Figs. 1a and 2c). For the limbs, although it is generally accepted that the proprioceptive input projects to the somatosensory cortex [Prud'homme and Kalaska, 1994], there is also evidence for processing of muscle spindle input in primary motor area four neurons [Lemon and

van der Burg, 1979; Mima et al., 1997]. It is therefore possible that a motor projection also exists for the eye proprioceptive input. Eye position information, which combines eye proprioception with the efferent copy of the motor command [Bridgeman and Stark, 1991; Gauthier et al., 1990], reaches the premotor cortex where it modulates the response of this area to visual stimuli [Baker et al., 1999; Boussaoud et al., 1998]. We suggest therefore that the extension of the proprioceptive signal into the premotor cortex found here may provide a proprioceptive eye position signal to be combined with the efference copy of the oculomotor command and visual input.

The suprathreshold voxels in the hemisphere contralateral to the stimulated eye were located inferior to the sensorimotor hand area. Mean z-coordinate for eye proprioception representation = 41 mm superior to the AC-PC line, whereas for the hand represenation mean z-coordinate was 55 mm. This is compatible with the well-known organization of the somatosensory homunculus and also with our previous result showing a functional impairment of proprioception for the right eye after TMS targeted posterior and inferior from the motor hot spot for the right hand [Balslev and Miall, 2008]. The brain area whose activation using TMS is most likely to produce a muscle twitch in the hand (the motor hotspot) lies approximately 4 mm anterior and 1 mm medial relative to the peak fMRI activation caused by index finger movement [Sparing et al., 2008]. This result, together with our coordinates of the peak activation for the right hand (x, y, z = −46, −6, 56 mm; Table II), places the TMS hotspot for the right hand in the left hemisphere at the approximate coordinates (x, y, z = −45, −2, 56 mm). Thus, the motor hotspot for the hand lies 12 mm anterior and 16 mm superior from the peak activation for the right eye in the left hemisphere (x, y, z = −36, −16, 40 mm; Table I). The straight-line distance between the TMS motor hotspot and the proprioceptive eye representation identified with fMRI is therefore 23.5 mm. This matches well with the 3 cm scalp distance between the motor hotspot for the right hand and the TMS targeting of the proprioceptive eye representation [Balslev and Miall, 2008].

These fMRI results are also consistent with the neurophysiological recordings in the monkey that showed a proprioceptive eye representation in the depth of the central sulcus of the contralateral hemisphere. Furthermore, we show that the proprioceptive eye representation is not limited to the hemisphere contralateral to the eye, but extends to the ipsilateral hemisphere, at a symmetrical location. This bilateral representation contrasts with the proprioceptive representation of the hand which is limited to the contralateral hemisphere [Mima et al., 1999] and resembles the organization of the frontal eye fields, in that each eye is represented in both hemispheres [Blanke and Seeck, 2003; Rafal, 2006]. In primates both eyes normally fixate the same target to provide a merged visual percept and stereopsis. Therefore, an integration of EOM proprioceptive signals across the two eyes is likely. Altering proprioception from one eye by passive rotation changes the perceived position of the other eye [Gauthier et al., 1990] further supporting the integration of eye position signals across the two eyes. The representation of EOM proprioception from both eyes next to each other in each hemisphere may provide the anatomical substrate for this functional integration.

In summary, this study identified the human proprioceptive EOM representation in the sensorimotor cortices of both hemispheres. This bilateral representation in the somatosensory cortex extending into the premotor cortex may serve the integration of eye position signals from the two eyes and with the efferent copy of the oculomotor command. The identification of the brain areas involved in the perception of eye position in humans may now allow precise targeting of these areas in intervention studies (e.g. using TMS) to probe the function of eye proprioception.

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