Brief Communications

Eye Proprioception Used for Visual Localization Only If in Conflict with the Oculomotor Plan

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Both the corollary discharge of the oculomotor command and eye muscle proprioception provide eye position information to the brain. Two contradictory models have been suggested about how these two sources contribute to visual localization: (1) only the efference copy is used whereas proprioception is a slow recalibrator of the forward model, and (2) both signals are used together as a weighted average. We had the opportunity to test these hypotheses in a patient (R.W.) with a circumscribed lesion of the right postcentral gyrus that overlapped the human eye proprioceptive representation. R.W. was as accurate and precise as the control group ($n = 19$) in locating a lit LED that she viewed through the eye contralateral to the lesion. However, when the task was preceded by a brief (<1 s), gentle push to the closed eye, which perturbed eye position and stimulated eye proprioceptors in the absence of a motor command, R.W.'s accuracy significantly decreased compared with both her own baseline and the healthy control group. The data suggest that in normal conditions, eye proprioception is not used for visual localization. Eye proprioception is, however, continuously monitored to be incorporated into the eye position estimate when a mismatch with the efference copy of the motor command is detected. Our result thus supports the first model and, furthermore, identifies the limits for its operation.

Introduction

Without knowledge of eye position it would be difficult to match a person and a voice in a crowd, to plan an eye movement toward a salient noise or to reconstruct the spatial relationships in a visual scene from retinal snapshots. Despite a century-long debate about efference copy versus sensory reafference the question whether visual localization relies on the corollary discharge (von Helmholtz, 1925) or eye proprioception (Sherrington, 1918) is still unanswered and experimental observations seem contradictory. On one hand, the CNS receives proprioceptive eye position information—e.g., humans are aware of the passive displacement of the eyes in darkness (Skavenski, 1972)—and altering this proprioceptive information consistently leads to errors in visual localization (Campos et al., 1986, 1989; Gauthier et al., 1990; Bridgeman and Stark, 1991; Allin et al., 1996; Lennerstrand et al., 1997; Balslev and Miall, 2008). This line of evidence suggests that the afferent, proprioceptive input contributes to the estimate of eye position. On the other hand, in the monkey, bilateral section of the trigeminal nerves, which carry ocular proprioceptive information to the brain (Porter et al., 1983), does not reduce the accuracy or the precision of open-loop pointing (Lewis et al., 1998), suggesting that the efference copy is sufficient and eye proprioception not necessary for visual localization.

Prompted by the recent discovery of an eye proprioceptive signal in area 3a in the monkey (Wang et al., 2007; Xu et al., 2011) and in the postcentral gyrus in humans (Balslev and Miall, 2008; Balslev et al., 2011) we have re-examined the question of whether eye proprioception contributes to locating stimuli in relation to the body in a patient (R.W.) with a focal lesion of the postcentral gyrus. Her lesion overlapped the proprioceptive representation of the extraocular muscles from both eyes as previously identified with fMRI in healthy humans (Fig. 1) (Balslev et al., 2011). A deficit in eye proprioception was therefore presumed.

Visual localization was tested in darkness and monocularly using a task where the subjects had to place an LED straight in front of the nose (Gauthier et al., 1990; Balslev and Miall, 2008) under two conditions, "baseline" and "push." In one of these conditions (push) before each trial, a perturbation was applied briefly to the eye. A brief and gentle push applied on a nonviewing eye perturbs temporarily eye position without triggering a motor command (Ilg et al., 1989). In the absence of an efference copy, accurate eye position knowledge requires eye proprioception. Previous observations have shown that healthy subjects have no problem correcting for this perturbation. Their error in this condition was similar with that during the condition where no push was applied (baseline) (Balslev and Miall, 2008). If eye proprioception is incorporated into the eye position estimate we predicted that the patient will be less accurate and precise than the age-matched, healthy control group ($N = 19$) in either condition. On the other hand, if proprioception is important only in condi-

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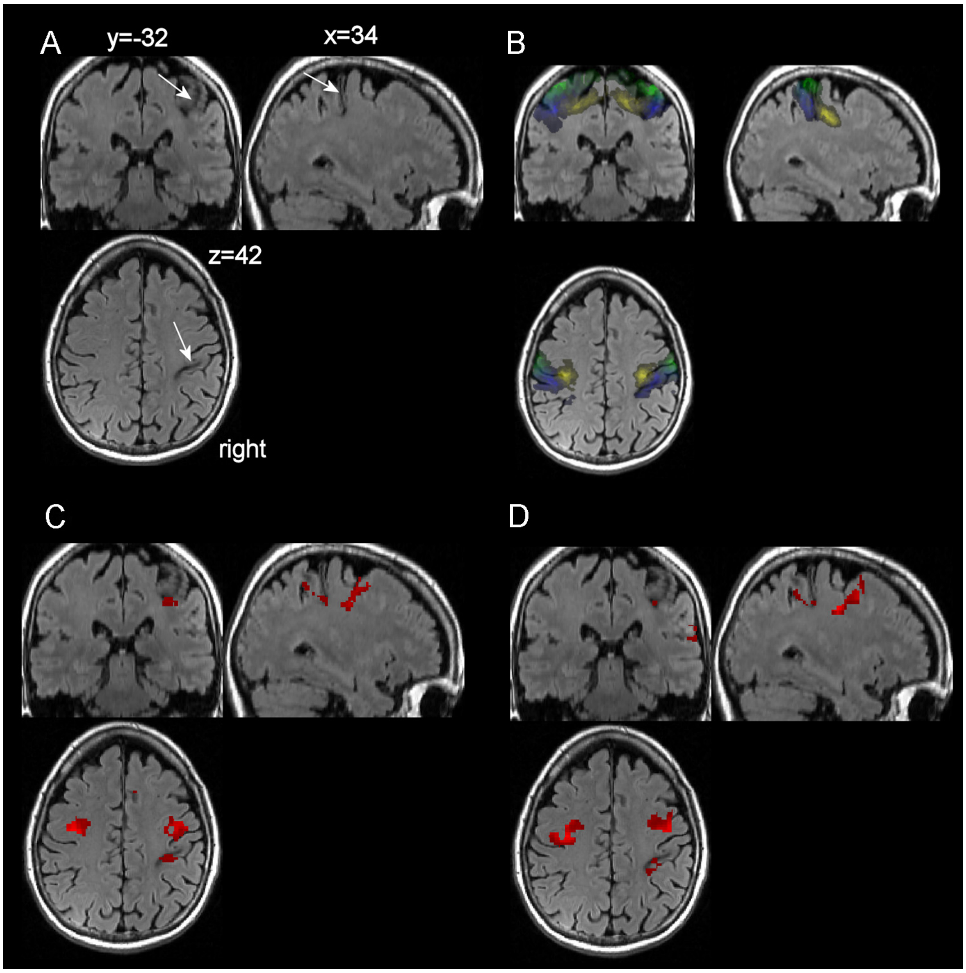

Figure 1. The lesion of patient R.W. overlaps with the Brodmann Areas 3a, 1 and 2 and the cortical projection for eye proprioception in the postcentral gyrus. The lesion (arrow) is shown in 3 orthogonal projections through the coordinates (*x*, *y*, *z* = 34, −32, 42) on a T1-weighted MR-image of the patient's brain normalized to the MNI space (***A–D***). In ***B***, the color overlays show the probabilistic atlas for area 3a (yellow), 2 (blue), and 1 (green), probabilities 10–100%. The red overlay shows the representation of eye proprioception for the left (***C***) and the right (***D***) eye muscles as identified by fMRI in a group of 18 healthy subjects (Balslev et al., 2011). The threshold for this functional overlay is *z*-score >2.61, $p < 0.005$, uncorrected for multiple comparisons.

tions when eye position is perturbed by an external force, then such errors should occur only in the condition with a push.

Materials and Methods

Subjects

Patient R.W. We tested the patient R.W., a 69-year-old woman, right-handed (Edinburgh handedness inventory score of 90; Oldfield, 1971) and with right eye dominance ("hole in the paper" test; Crider, 1944). Her vision was corrected to normal using glasses. R.W. had a MR-confirmed focal intracerebral hemorrhage with a length diameter of 3.6 cm centered on the right postcentral gyrus. The lesion overlapped with Brodmann Areas 3, 2, and 1 as defined by the Juelich atlas (Geyer et al., 1996; Grefkes et al., 2001; Eickhoff et al., 2005). On this atlas it was possible to localize 94.6% of the lesion volume, 80% of it being located in the primary somatosensory cortex (39.9% in Area 2, 19.7% in Area 3b, 15.9% in Area 1, and 4.5% in Area 3a). Less than 4% of the voxels were also found in Area 7 (3.9%), Area 4 posterior (3.2%), IPC (2.9%), and Area 4 anterior (2.8%). The lesion also overlapped in part with the projection of eye muscle proprioception in the sensorimotor cortex identified in healthy subjects by Balslev et al. (2011) (Fig. 1).

At the time of testing, ~3 years poststroke, R.W. had a selective proprioceptive deficit in both hands, but normal two-point discrimination and no impairment in the ability to move or exert power (Borchers et al., 2011). Similar with the hand, we found no asymmetry in the accuracy of tactile discrimination in the eyelid region. Two-point discrimination was identical on both sides, 16 mm on the lower and 20 mm on the upper eyelid. She reported that immediately after stroke she suffered from double vision, a symptom that resolved within a few days.

Control group. Nineteen healthy participants (15 women) were tested as controls (median age: 63 years, range 57–73 years). The mean age was not significantly different to the patient's age [*t* test, single case comparison (Crawford and Howell, 1998), $p = 0.394$]. All controls were right-handed and had normal or corrected-to-normal vision. Fifteen participants had right eye dominance. Patient and controls gave written informed consent to participate in the study, which was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and approved by the local Ethics Committee.

Visual localization task

Baseline condition. To investigate the effect of a lesion of the right postcentral gyrus on perceived eye position we used a task in which the participants located their visual straight ahead in monocular vision and darkness (Gauthier et al., 1990; Balslev and Miall, 2008).

The participant sat at 49 cm in front of an array with 96 LEDs separated by 1 cm/1.1°, its center aligned with the head/body midline. The head was fixed with a chin rest and cheek pads.

At the initiation of each trial one of 6 possible LEDs chosen in a predetermined random order that was identical across patient and controls was lit up (position −16.5°, −13.2°, −9.9°, 9.9°, 13.2°, 16.5°; negative values denote locations to the left of head midline). The participants' task was to navigate this LED directly in front of their nose by telling the experimenter to move the LED to the left or right. This position was recorded and a new trial started. The task comprised 24 trials, 4 for each possible start position of the LED. Visual localization error and SD were calculated.

Passive eye displacement (push) condition. To investigate the impact of eye proprioception on visual localization, the same task was performed immediately after a displacement of the viewing eye using a gentle and brief push (<1 s) on the closed eyelid. When applied to a closed eye this push moves the eye briefly in the direction of the push, then the eye returns toward its resting position. Because no eye movement occurs in the other eye (Ilg et al., 1989), it is unlikely that this maneuver causes an oculomotor command, and thus, the only source of information about the displacement is the extraocular muscle proprioceptors. The push condition was practiced with normal binocular vision before the start of the experiment. The participants placed their right index finger at the outer corner of the eyelid and pushed the eye bulb toward the nose, increasing the force until they produced double vision. They were instructed to reproduce the same force when pushing the eye through a closed eyelid during the experiment. Immediately after pushing the eye, the participants opened their eye to perform the task like in the baseline condition. Twelve trials per eye (two for each starting LED) were performed. For both eyes, participants pushed with their right index finger. Patient and controls performed the conditions in the same order: right eye baseline, right eye push, left eye baseline, and left eye push.

Analysis

To compare R.W.'s performance in one task with the control group, we applied two-tailed *t* tests adapted for the single-case studies (Crawford and Howell, 1998). To test for a dissociation between conditions in patient R.W. an unstandardized difference test was used. This test implements a repeated-measures ANOVA for the single-case (Crawford et al., 1998; Crawford and Garthwaite, 2005).

Results

In the baseline condition, both R.W. and the control group were accurate in locating the straight ahead position visually with either eye (Fig. 2*A*,*B*). The modified *t* test for the single-case comparison (Crawford and Howell, 1998) showed no significant difference between R.W. and the control group ($p > 0.6$ for left eye; $p > 0.7$ for right eye). Moreover, there was also no statistical evidence for an accumulation of errors in the patient from the first to the last trial of the baseline session. The regression line encoding the change in error over time had a small negative slope in the patient (-0.18 for the left and -0.15 for the right eye) that did not significantly differ from the control group ($p > 0.2$ for either eye).

In the push condition, the accuracy of visual localization in the control group was similar to the baseline condition. In contrast, R.W. showed a significant error to the left by 15.91° for the left, contralesional, eye, which was significantly different from the control group ($p = 0.049$). For the right eye, no significant difference between R.W. and the control group ($p > 0.9$) was observed. A repeated-measures ANOVA implemented as an unstandardized difference test (Crawford et al., 1998; Crawford and Garthwaite, 2005) showed a highly significant difference between conditions in the patient relative to controls for the left eye (unstandardized difference test $p < 0.001$, correlation between baseline and push conditions in the control group $r = 0.92$) and no significant interaction for the right eye ($p > 0.7$, correlation between conditions in the control group $r = 0.73$). The left, contralesional eye was significantly more affected than the right, ipsilesional eye. In the push condition, there was a significant difference between the left and the right eye in the patient compared with controls (unstandardized difference test, $p = 0.043$, correlation between eyes in the control group $r = 0.49$).

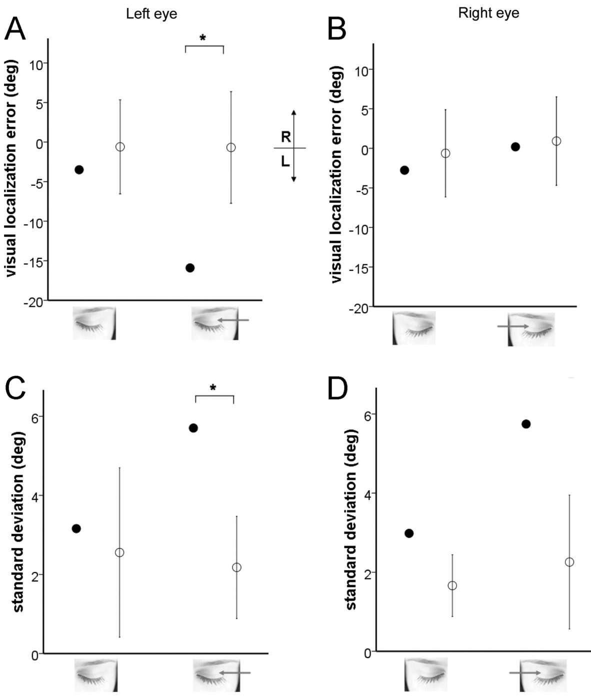

Figure 2. Accuracy and precision for locating an LED relative to the body in monocular vision and in darkness. Mean error (***A***, ***B***) and SD (***C***, ***D***) for the patient and a group of 19 healthy controls are shown in baseline and in push condition, separately for the left eye (***A***, ***C***) and right eye (***B***, ***D***). Error bars represent one SD. The arrow on the *x*-axis label shows the direction of the push. Filled circles, patient; empty circles, controls; asterisk denotes a *p* value <0.05 for a single-case *t* test testing for a difference between the patient and the control group ($N = 19$).

Results in the same direction albeit weaker were found for the SD (Fig. 2*C*,*D*). Again no difference was found between patient and controls in the baseline condition (single-case comparison: $p = 0.786$ for left and $p = 0.117$ for right eye). For the left eye, the push significantly increased the SD in the patient (Fig. 2*C*, $p = 0.016$). For the right eye, a numerical difference in the same direction was found (Fig. 2*D*, $p = 0.06$). The difference between conditions in the patient however did not reach statistical significance for either eye (unstandardized difference test $p > 0.1$, correlation $r = 0.46$ for the left eye and $r = 0.64$ for the right eye).

Discussion

This study investigated whether eye proprioception contributes to visual localization. We tested whether a patient with a presumed deficit in eye proprioception after a focal lesion in the left postcentral gyrus made more errors in locating a visual target relative to the head midline compared with an aged-matched control group. Although the patient was as accurate and precise as the control group under the normal, baseline condition, she exhibited a significant error when the position of one eye was perturbed peripherally. In this condition, we found a shift to the left in perceived straight ahead when the task was executed with the left, contralesional eye. This corresponds to a shift toward the nose in perceived eye position, in the direction of the applied force. The direction of this shift is identical with that produced by a push after 1 Hz rTMS in healthy subjects, a procedure that decreased the excitability of the eye proprioceptive area (Balslev and Miall, 2008). The illusory eye rotation induced by peripheral eye manipulation that occurs only in the context of a decreased cortical processing in the somatosensory cortex suggests that under these circumstances, an erroneous proprioceptive input is incorporated into the estimate of eye position.

The impairment in visual localization in the patient during the push condition was stronger for the left, contralesional eye. For this eye both accuracy and precision were decreased in the patient relative to the control group. For the right, ipsilesional eye, the mean error was similar with the control group whereas for the SD we found a trend ($p = 0.06$) for a decrease in the precision for visual localization, similar with the left eye. Thus, despite the bilateral representation of eye proprioception in the human brain identified by fMRI (Balslev et al., 2011), the larger severity of the proprioceptive impairment in the contralesional compared with the ipsilesional eye suggests that the eye proprioceptive representation in the contralateral hemisphere has a higher functional impact.

Based on these results we argue that in normal conditions the oculomotor command is sufficient for visual localization and proprioception adds no benefit. However, the proprioceptive input seems to be used as soon as it conflicts with the estimate of eye position based on the efference copy. In this way, the healthy control group can correct for an externally imposed perturbation to eye position. In the patient with a somatosensory lesion, this information is reduced or distorted. Consequently errors in visual localization occur when the oculomotor command alone cannot indicate eye position, as in the push condition of the present experiment.

This interpretation explains previously contradictory observations. On one hand acute distortions in eye proprioceptive input after tendon vibration (Allin et al., 1996; Lennerstrand et al., 1997), passive eye movement (Gauthier et al., 1990; Bridgeman and Stark, 1991) or rTMS (Balslev and Miall, 2008) in humans alter visual localization, suggesting that proprioception contributes to this function. These observations would fit with a model where the two sources of eye position are combined as a weighted average, the weight of proprioception being calculated to be ~26–32% (Gauthier et al., 1990; Bridgeman and Stark, 1991). On the other hand, in the monkey, the reduction of the proprioceptive afference to the brain by bilateral sectioning of the trigeminal nerve does not increase either error or SD for locating a visual target during open-loop pointing (Lewis et al., 1998) suggesting that proprioception makes no contribution at all. These observations would fit with a model where proprioception, although not used for visual localization, calibrates over the long term the forward model which estimates the consequences of the oculomotor command (Steinbach, 1986). Because these two sets of experiments were performed in different species with known differences in the eye proprioceptive system (e.g., extraocular muscle spindles are absent in the monkey but present in humans; Donaldson, 2000), interspecies differences could have been responsible for the apparent contradiction between their conclusions. Another possible source of discrepancy is the concern that in the experiment by Lewis et al. (1998), despite the bilateral section of the trigeminal nerves, sufficient proprioceptive input could reach the CNS via the oculomotor nuclei, which have recently been suggested to receive sensory input from the pallisade endings (Lienbacher et al., 2011). The current experiment tested in the same subjects how visual localization is affected by both the conflict between the proprioceptive inflow and the efference copy (e.g., by comparing the baseline and the push condition) as well as by the reduction in the proprioceptive afference (e.g., by comparing the patient and the healthy group). This design allowed us to conclude that although in normal conditions proprioception is unlikely to contribute to visual localization, the afferent input is compared with the efference copy and used as soon as a discrepancy between the two sources of eye position information is detected. Our observations offer thus support to both models and furthermore explain their apparent contradiction by identifying the circumstances when they operate.

The redundancy of proprioception for eye localization is at the first glance surprising. It contrasts with the findings in the skeletal system, where limb localization relies on both proprioception and the efference copy of the motor command (Wolpert et al., 1995). It is also at odds with the idea that the brain uses all available information, weighting each source according to its reliability to obtain a common, more precise estimate (van Beers et al., 2002; Ernst and Bülthoff, 2004). Unlike the limbs that move in a relatively unpredictable environment, against gravity and at lower speed, the eyes move very fast during saccades, rest on the orbit floor cushioned in connective tissue and are unlikely to be exposed to sudden mechanical perturbations. Therefore, for the eye, neural mechanisms may have evolved to support precise feedforward control of position, rendering the slower proprioceptive feedback superfluous. However, proprioceptive information is sampled, compared with the efference copy and incorporated into the estimate of eye position as soon as discrepancies are detected. This could be the case after injury or surgery or after small mechanical perturbations of the eye bulb (e.g., applying a contact lens).

Our conclusion rests on the assumption that the comparison between the proprioception and efference copy occurs upstream S1, so that despite an S1 lesion, a mismatch between the two signals (e.g., eye push) can be correctly detected and can impact on visual localization. In humans, the ascending pathways for neither the proprioceptive input nor the efference copy of the oculomotor command are known. Single cell recordings in nonhuman primates have uncovered a pathway that relays the efference copy from the superior colliculus via the medial-dorsal thalamic nucleus to the cortex (Sommer and Wurtz, 2008). For eye proprioception, the subcortical pathways are less well understood, but similar with those for the efference copy, are likely to include the superior colliculus (Ndiaye et al., 2000) or the central thalamus (Tanaka, 2007), structures which are therefore plausible candidates for where the two signals converge. However, mapping the neural structures that respond to the mismatch between proprioception and efference copy (e.g., by fMRI or neurophysiological recordings) would be needed to identify how the CNS implements this comparison.

One could object that the weighted average model could explain the current data if one assumes that proprioception is weighted higher in the push compared with the no-push condition. In the push condition, this would then cause a larger difference in performance between controls and the patient, who has no proprioceptive signal, and therefore makes more systematic error and drops precision. Our arguments against this objection are the failure to find a difference in SD between patients and controls in the no-push condition as well as the similar SD in controls between the push and no-push conditions. However, since these are both null results, they should be interpreted with caution. It may be the case that the weight of proprioception in the no-push condition is so small, that the corresponding small increase in noise in the patient is swamped by other noise sources, such as output errors in aligning the stimulus to straight ahead. A similar explanation could be given for the failure to find a statistically significant increase in SD in the control group from the no push to the push condition. To test this possibility further studies using different visual localization tasks (e.g., pointing or saccades to visual targets), various target positions (e.g., not only straight ahead) or various delays between the push and the task would be needed.

In conclusion, the current data suggest that visual localization normally relies on the efference copy of the motor command, and that eye proprioception, although continuously monitored, is used only in conditions when these two sources of information mismatch.

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