Proprioceptive deafferentation slows down the processing of visual hand feedback

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During visually guided movements both vision and proprioception inform the brain about the position of the hand, so interaction between these two modalities is presumed. Current theories suggest that this interaction occurs by sensory information from both sources being fused into a more reliable, multimodal, percept of hand location. In the literature on perception, however, there is evidence that different sensory modalities interact in the allocation of attention, so that a stimulus in one modality facilitates the processing of a stimulus in a different modality. We investigated whether proprioception facilitates the processing of visual information during motor control. Subjects used a computer mouse to move a cursor to a screen target. In 28% of the trials, pseudorandomly, the cursor was rotated or the target jumped. Reaction time for the trajectory correction in response to this perturbation was compared under conditions with normal and reduced proprioception after 1-Hz rTMS over the hand-contralateral somatosensory cortex. Proprioceptive deafferentation slowed down the reaction time for initiating a motor correction in response to a visual perturbation in hand position, but not to a target jump. Correlation analyses suggested that reaction time was influenced by the size of the visual error rather than the visuo-proprioceptive conflict or the variance in cursor position. We suggest that during movements intact proprioception is necessary for the rapid processing of visual feedback.

Keywords: visual, proprioceptive, motor control, multisensory interaction

Introduction

Current models for visuo-proprioceptive integration assume a fusion of visual and proprioceptive information in the spatial domain, with a bimodal estimate lying between the two merged, unimodal estimates (Rossetti, Desmurget, & Prablanc, 1995; Sober & Sabes, 2003; van Beers, Sittig, & Gon, 1999). In the literature on perception, however, there is evidence that different sensory modalities also interact in the temporal domain, so that a stimulus in one modality can speed up the reaction to a stimulus in a different modality when the stimuli are presented in spatial proximity (Spence, McDonald, & Driver, 2004). For instance, a key press in response to a flash of light occurs faster if a non-informative cue in a different modality is presented shortly before the visual stimulus near its location compared with far away (Kennett, Eimer, Spence, C., & Driver, 2001; Spence & Driver, 1994). This facilitation of a response to a cued stimulus has recently been shown to reflect the enhancement of visual signal by increased attention at the cued location (McDonald, Teder-Sälejärvi, & Hillyard, 2000).

During visually guided movements, visual and proprioceptive stimuli of hand location normally occur in spatial and temporal correspondence. There is general consensus that visual information reaches the CNS slower than information coming through other modalities due to the delay introduced by transduction processes in the retina's photoreceptors. Whereas the current models specify how vision and proprioception interact spatially, very little is known about their temporal interaction. We therefore tested whether proprioception speeds up the processing of visual information during a reaction time motor task. We measured whether errors in the visual hand position induced by a small rotation transformation were corrected more slowly in a condition with decreased proprioceptive accuracy. The proprioceptive deafferentation was induced in healthy subjects by 1-Hz rTMS over the somatosensory cortex (Balslev et al., 2004).

To test for nonspecific effects of proprioceptive deafferentation on the reaction time for a motor response, the subjects also completed a control task where they corrected for a target jump, a task that does not require visual feedback from the hand (Pélisson, Prablanc, Goodale, & Jeannerod, 1986). The absence of a reaction time difference in this control task would exclude a

general decrease in reaction time after proprioceptive deafferentation.

There are several ways in which interactions between visual and proprioceptive signals could influence reaction times in this task.

Firstly, the spatial fusion of visual and proprioceptive estimates into a single estimate of hand location that lies in between the visual and the proprioceptive ones (Rossetti et al., 1995; Sober & Sabes, 2003; van Beers et al., 1999) would predict a decrease in reaction time after proprioceptive deafferentation. This is because by reducing the proprioceptive input, the combined signal would be shifted toward the visual estimate, and thus the visual error would be more pronounced (Hypothesis 1).

Secondly, if the spatial reliability of the combined signal is considered (van Beers, Baraduc, & Wolpert, 2002), then the opposite effect may be seen. The combined estimate of hand position based on two independent noisy estimates is normally more reliable than either estimate alone. If the effect of deafferentation was to increase noise in the proprioceptive channel beyond the capacity of this mechanism for noise reduction, then the combined estimate of the hand position would become less reliable. Hence, it may take longer to perceive the deviation of the trajectory away from the target, and thus the reaction time to correct the movement would be elevated (Hypothesis 2).

Thirdly, if the two sensory modalities interact in the spatial allocation of attention (McDonald et al., 2000), such that proprioception involuntarily draws attentional resources to the location of the visual stimulus, then proprioceptive deafferentation should slow down the response to a perturbation in visual feedback, as the visual information would be less salient without the proprioceptive cue (Hypothesis 3).

Finally, if the visuo-proprioceptive conflict rather than the visual error triggers a trajectory correction, when this conflict is reduced by proprioceptive deafferentation, the reaction time for the correction is expected to increase (Hypothesis 4).

Thus, an increase in reaction time after proprioceptive deafferentation would support Hypotheses 2, 3, or 4, whereas a decrease in reaction time would support Hypothesis 1. In addition, to find out which factors control the reaction time for a trajectory correction and thus to be able to separate between Hypotheses 2, 3, and 4, we also computed correlation coefficients between this reaction time and measures of visual reliability, visual error, and visuo-proprioceptive conflict.

Methods

Subjects

Ten healthy, right-handed subjects participated (five males). Their median age was 22.5, range 18–49. All subjects had normal or corrected to normal vision and used a computer mouse daily. All subjects gave written informed consent to participate in the study, which was approved by the School of Psychology Ethics Committee at the University of Birmingham.

Task

The participant sat comfortably at a table. A computer screen (300 × 220 mm, 640 × 480 pixels) was placed at 50 cm in front of him/her. With their dominant hand index finger, the participant operated a sliding computer "mouse" (FELIX Pointing Device, Altra, Rawlins, WY), which moved in an active area of size 30 × 24 mm. We used this small mouse to enable the subjects to perform all movements using their index finger because the TMS procedure used in these experiments has previously shown to reduce index finger proprioception (Balslev et al., 2004). The mouse controlled a screen cursor (filled white square, 20 × 20 pixels, visual angle = 1.1°). The hand was hidden from view by a plastic screen.

At the start of each trial the mouse and cursor were placed in the start position, situated in the upper right corner (Figure 1). A target (empty red square, 30 × 30 pixels, pen width 5 pixels, visual angle 1.65°) appeared always at 480 pixels from the start position. The ideal trajectory from the start point to the target was a line (invisible) oriented at 45° from horizontal. The subjects were instructed to move the cursor to the target as fast and as accurately as possible. They were also told that the cursor trajectory or the target position could be perturbed and that they had to correct for the perturbation and try to land the cursor on target. Each trial lasted for 1 s. After the end of the trial, the target disappeared from the screen and the subjects placed the cursor back to the start position at their own pace. The next trial would start as soon as they reached the start position.

In 28% of the trials, we pseudorandomly introduced a movement perturbation that could be either a 20° rotation of cursor trajectory relative to the trajectory of the mouse or a target jump of 20° along an arc centered on the start position (9° visual angle). Either perturbation was initiated at the onset of movement, when the cursor moved 3 pixels away from the start box. Both clockwise and counterclockwise perturbations were applied in random order. There were two different types of trial blocks, with either cursor rotation or target jump trials; subjects were informed of which perturbation to expect at the start of each block. Each subject completed two identical sessions. Each session consisted of four blocks with 50 trials each, alternating between blocks with cursor rotation and target jumps. The order of block presentation was counterbalanced
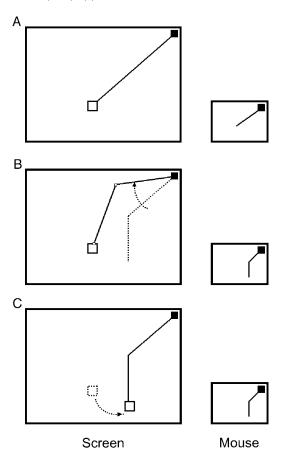
Figure 1. Schematic representation of the task. (A) Unperturbed trial; (B) trial with a 20° clockwise rotation of cursor trajectory relative to the trajectory of the mouse; (C) trial with a counter-clockwise target jump of 20° along an arc centered on the start position. ■—start position for screen cursor and mouse; □—screen target. Target position and cursor/mouse trajectory without the perturbation are shown with dashed lines and after the perturbation with solid line. The arrows indicate the direction of the perturbation.

across subjects. rTMS was applied at rest, in between the two sessions.

A PC laptop running E-prime (Psychology Software Tools, Inc., Pittsburgh, PA) under Windows 2000 presented the stimuli and recorded the position of the mouse and cursor every 20 ms.

The subjects rested their head on a chin support. Each rTMS session consisted of 900 biphasic stimuli produced by a Magstim Rapid stimulator (Dyfed, UK) and delivered with a frequency of 1 Hz over 15 min. One of two identical, standard 70-mm diameter figure-of-eight coils was centered over the stimulation site and was maintained in this position by a coil holder. This site was mapped in each subject in relation to the "motor hotspot" of the left hemisphere, which is the scalp projection of the primary motor cortex (Wassermann et al., 1996). The site of stimulation was located at 3 cm posterior to the motor hotspot, measured on a line oriented at 45° from the

sagittal plane and perpendicular on the central sulcus. This protocol has previously been shown to result in a decrease of proprioceptive accuracy in the right hand (Balslev et al., 2004). The motor hotspot was defined as the point of maximum evoked motor response in the relaxed first dorsal interosseus (FDI) muscle of the right hand. Stimulation intensity was set at 110% of resting motor threshold of the right FDI muscle. To identify the resting motor threshold, we asked the subjects to rest the right hand on the table with the fingers slightly spread. The resting motor threshold was defined as the lowest intensity that reliably elicited a visible twitch in the FDI muscle when the stimulation was given over the motor hotspot. Each subject did two sessions, with real and sham rTMS. During real rTMS, the coil was positioned tangential to the scalp with the long axis of the figure-of-eight coil oriented at 45° to the parasagittal plane. The current flow of the initial rising phase of the biphasic pulse in the TMS coil induced a current flowing from posterior to anterior in the brain. During sham rTMS, the coil was tilted at 90° to the scalp, with one wing of the coil in contact with the scalp over the site of stimulation. This coil arrangement reproduces the acoustic sensation of real rTMS, with minimal effects on the cortex (Lisanby, Gutman, Luber, Schroeder, & Sackeim, 2001). During each session, the active coil was exchanged for the spare coil after 4 and 11 min of rTMS to avoid overheating. All subjects completed their testing within 10 min after the last rTMS pulse.

Analysis

The velocity time series were smoothed with a second order 5-Hz low-pass Butterworth filter. Then the time bin for peak acceleration in lateral direction after the maximum tangential velocity was found and reaction time for the error correction was calculated as the difference between this time bin and the time bin for movement onset. Trials were discarded if velocity at this time bin was under 50 pixel/s (1 pixel/time bin) or if the position of the cursor at this time bin was more than 100 pixels off-diagonal. These criteria ruled out trials where the subject was too late in correcting and had already slowed their finger movement or trials where the subject failed to move toward the initial target position.

Normalization procedure

Because of the large standard deviation in the reaction time data across subjects, we performed the analyses on normalized rather than absolute reaction times. This was done by subtracting the pre-TMS baseline reaction time from the post-TMS reaction time. The normalization to the pre-TMS baseline within each session also eliminated nonspecific effects such as the level of attention.

Correlation analyses

To find out whether a trajectory correction during trials with a cursor rotation was triggered by the visuo-proprioceptive conflict or the visual error, we computed the Pearson's correlation coefficient between the reaction time for a trajectory correction and (1) the distance between the cursor and the mouse at the time bin of trajectory correction, which measures the visuo-proprioceptive conflict, and (2) the distance between the cursor and the ideal trajectory at correction time as a measure for the visual error. The ideal trajectory was defined as the straight line from start position to the target. We collected approximately 84 values for each subject from all valid trials with a cursor perturbation and normal proprioception (pre- and post-Sham and pre-TMS sessions, each session with approximately 28 valid trials). The correlation coefficient was calculated within each subject across all 84 trials, then the correlation coefficient was tested across subjects using a one-sample *t* test.

We had the following predictions. First, a negative correlation between reaction time and visuo-proprioceptive conflict would mean that a large visuo-proprioceptive conflict is associated with a short reaction time for a correction. This would support the idea of a causal link between the visuo-proprioceptive conflict and a trajectory correction. The opposite result—a positive correlation between reaction time and visuo-proprioceptive conflict—would mean that the longer the reaction time for a correction, the larger the visuo-proprioceptive conflict. This would occur, for instance, if long reaction times are associated with longer trajectories up to the point of correction and therefore with a large visuo-proprioceptive conflict. This would not support the idea of a causal link between the visuo-proprioceptive conflict and a trajectory correction.

Second, a negative correlation between reaction time and visual error would be expected, if large visual errors are detected earlier and thus lead to shorter corrective reaction times. This would support the idea of a causal link between the visual error and a trajectory correction. The opposite result—a positive correlation between reaction time and visual error—would mean that the longer the reaction time taken for a correction, the longer time there would be for error to accumulate. This would not support the idea of a causal link between visual error and trajectory correction.

In the cursor rotation condition, the distance between cursor and mouse is proportional to the distance traveled, that is, the product between movement speed and reaction time for the correction. Therefore, the further the point of correction from the start position, the larger the visuo-proprioceptive discrepancy. Thus, one might assume that if movement speed is approximately constant, there would be an unavoidable positive correlation between the visuo-proprioceptive conflict and the reaction time. To make sure that this is not the case, we have also computed the correlation coefficient between average movement speed up to the point of correction and reaction time for the cursor-rotated trials. The correlation coefficient was calculated within subject using approximately 84 values (three sessions of about 28 trials each, the same non-TMS sessions, and trials as above) then tested across subjects using a single-sample *t* test.

To find out whether a decrease in spatial reliability of cursor position after deafferentation caused the increase in reaction time, we calculated the Pearson's correlation coefficient between the reaction time for a trajectory correction and the standard deviation in visual error, which was defined as the distance between the cursor and the ideal trajectory at the time bin of trajectory correction. We collected approximately 28 trajectories for each subject from all valid trials with a cursor perturbation after rTMS induced proprioceptive deafferentation (post-TMS sessions). For each subject, the standard deviation of the visual error was calculated across trials and reaction time was averaged across trials. These values were then normalized by subtracting the corresponding pre-TMS values. The correlation coefficient was computed across subjects and tested with a one-sample *t* test. A positive correlation between reaction time for a trajectory correction and standard deviation would support the idea that an increase in standard deviation, and hence a decrease in spatial reliability of visual hand position results in an increase in reaction times. A negative correlation between the reaction time and the standard deviation could for instance occur if subjects, with a higher level of uncertainty in their proprioceptive estimates and hence a higher standard deviation in the combined visual and proprioceptive bimodal estimate, were able to assign a higher weight to the visual channel in computing hand position, thus increasing the saliency of the visual error and decreasing reaction time for a correction.

Results

Sample trajectories are shown in Figure 2. Less than 5% of the perturbed trajectories were discarded. For trials with perturbed trajectories, the average movement time was 638 ms with an average velocity up to the point of trajectory correction of 65.9°/s of visual angle (1198 pixels/s). There was no significant difference after rTMS compared with sham in either of these variables for trials with a cursor rotation (paired-samples *t* tests, *p* values >.2) or target jump (*p* values >.7).

Mean reaction times before normalization are given in Table 1. rTMS over the somatosensory cortex prolonged the reaction time for a correction for cursor rotation by an average of 34 ms (Figure 3, Wilcoxon signed ranks test $Z = -2.5$, $p = .01$; the interaction between trial type [cursor vs. target perturbation] and intervention type [real or sham rTMS] was statistically significant, repeated
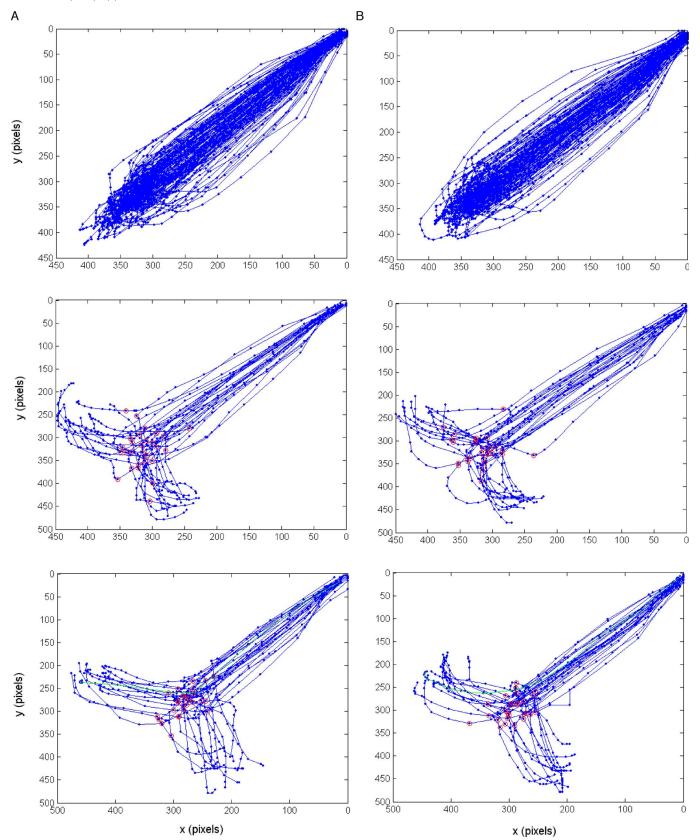
Figure 2. Sample finger trajectories. Trajectories from all trials with no perturbation (top row), cursor rotation (middle row), and target jump (bottom row) recorded before (A) and after rTMS (B) in one subject. Blue dots—mouse position. Red circles—time point for maximum acceleration in lateral direction after peak velocity, where a correction was assumed to be initiated. Valid trajectories—blue. Invalid trajectories—green.

	Pre-TMS	Post-TMS	Pre-Sham	Post-Sham	Pre-TMS	Post-TMS	Pre-Sham	Post-Sham
			Cursor				Target	
Mean	388	413	398	389	368	355	360	357
SD	48	60	45	58	22	24	23	26

Table 1. Mean and standard deviation for the absolute value of the reaction time (ms) across subject after the rTMS intervention in Experiment 1.

measures ANOVA $p = .006$). The difference in reaction time was calculated by entering the group average for the reaction time into this formula: (post-TMS − pre-TMS) − (post-Sham − pre-Sham).

The average within-subject correlation between the reaction time and the distance between mouse and cursor at the time when this correction was initiated (visuo-proprioceptive discrepancy) was +.41 (standard deviation across subjects, $SD = 0.22$). The average within-subject correlation between the reaction time and the visual error (distance between the cursor and the ideal trajectory at the time when a trajectory correction was initiated) was −.28 ($SD = 0.19$). Both were significantly different from zero (one-sample t tests, $p < .001$). The average correlation between movement speed and reaction time was −.74 ($SD = 0.09$), again significantly different from zero ($p < .001$).

The between-subjects correlation coefficient between the change in reaction time and the change in standard deviation of the visual error at the time of correction was −.75 and significantly different from zero ($p = .012$).

Discussion

Acute reduction in proprioception with rTMS lead to slower correction of visual feedback errors compared to
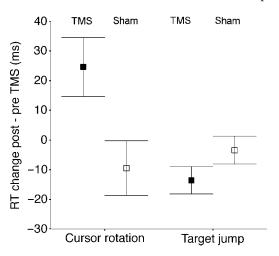

Figure 3. Increase in reaction time for cursor rotation after rTMS-induced proprioceptive deafferentation (mean ± *SE*); ■—real rTMS; □—sham rTMS.

reactions to step changes in target position. Because in these experiments the error in hand position appeared only in the visual modality, this result confirms that vision and proprioception interact during motor control (Rossetti et al., 1995; Sober & Sabes, 2003; van Beers et al., 1999). However, this result also suggests that vision and proprioception interact not only in the spatial domain, as found in this previous work, but also in the temporal domain, so that intact proprioception facilitates the processing of visual feedback of cursor position. When a visual feedback error is detected, a corrective response is made, and we argue without proprioceptive modulation of vision that these feedback errors are less quickly reacted to.

The increase in reaction time to correct for cursor-rotated errors rules out Hypothesis 1 in the Introduction section. In turn, this leaves the Hypotheses 2, 3, and 4. Correlation analyses rule out two of these explanations and provide support to the idea that the increase in reaction time after deafferentation reflects a decrease in the speed of visual processing of cursor position.

Hypothesis 2 was that a decrease in the reliability of the combined visual and proprioceptive estimate of visual hand position, after proprioceptive deafferentation, prolonged the reaction time for a trajectory correction. This might be expected if the subjects allowed more time before correcting their movements to accumulate more evidence in the estimated finger position. This is also unlikely because the change in reaction time and the change in standard deviation of cursor position error were negatively correlated across subjects, so that a decrease in reaction time was found in subjects where the standard deviation of the visual position error increased. Note that this analysis must be made across subjects, as calculation of standard deviations is not possible within single trials. However, by normalizing each subject's data to their pre-TMS levels, we rule out a trivial correlation between high variance and short reaction times that might be due to individual differences. We suggest that this argues against Hypothesis 2.

Hypothesis 4 was that the visuo-proprioceptive conflict rather than the visual error triggers a trajectory correction. In other words, the subjects detect the discrepancy between the cursor position and their finger position rather than an error between the cursor and the target. When this conflict is reduced by proprioceptive deafferentation, the reaction time for this correction would therefore increase. This is unlikely, given that the correlation between the visuo-proprioceptive discrepancy and the reaction time for a trajectory correction was positive (the longer the reaction

time for a correction, the larger the visuo-proprioceptive conflict). In contrast, visual error and reaction time were negatively correlated (the larger the visual error, the shorter the reaction time for a correction). Moreover, the negative correlation between reaction time and movement speed rules out the possibility that visuo-proprioceptive discrepancy and reaction time are positively correlated because of the trivial relationship between speed, distance, and time. Thus, we can rule out Hypothesis 4.

The negative correlation between reaction time and visual error supports the idea that the reaction time for a correction depends on the visual error. The increase in reaction time after proprioceptive deafferentation may thus reflect a slower detection of this visual error. We suggest that visual and proprioceptive channels facilitate each other, and rapid detection of visual feedback errors depends on an intact proprioceptive signal (Hypothesis 3).

Thus, the present results cannot be explained by the current model in which vision and proprioception combine into a single integrated and more reliable estimate of hand location that lies between the visual and the proprioceptive estimates (Rossetti et al., 1995; Sober & Sabes, 2003; van Beers et al., 1999). Vision and proprioception appear to interact not only in the spatial domain, as those reports previously demonstrated, but also in the temporal domain, with acute withdrawal of proprioception induced by rTMS slowing trajectory corrections in response to visual feedback. We do not know where exactly this interaction between proprioception and vision occurs in the chain of neural processes that lead from the perception of visual feedback to a corrective hand movement. One possibility is that proprioception involuntarily draws attentional resources to the location of the hand in visual space so enhancing the visual signal.

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