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RESEARCH ARTICLE

Evidence for stronger visuo-motor than visuo-proprioceptive conflict during mirror drawing performed by a deafferented subject and control subjects

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Abstract It has been proposed that mirror drawing is difficult because of the conflict between visual and proprioceptive signals from the arm. However, even without proprioception, there should be difficulties in planning movements to visual targets observed in a mirror, as the mirror-reversed spatial information must be translated into appropriate hand actions. Mirror drawing tasks suggest these planning conflicts are likely to be most obvious at corners, when encountering sharp changes in direction. We have therefore tested the speed of mirror drawing in a chronically deafferented man and in a control group of normal subjects, and hypothesized that increases in template complexity (number of corners) would result in reduced drawing speeds in all subjects. Indeed, all subjects, including the deafferented man, showed movement durations that increased linearly as the complexity of the drawings increased. However, the deafferented man was significantly faster than the control subjects at tracing curved templates. We suggest that the major difficulty in mirror tracking is in the visuo-motor planning of actions based on mirror-reversed visual information, and is not a conflict between visual and proprioceptive signals about arm motion.

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Introduction

Accurate movement of the hand requires not only knowledge about where to move to, but also about the current position and motion of the body, its motor state. Recent work has suggested that a weighted sum of all available information sources is used to generate this state estimate (Kording et al. 2004; van Beers et al. 1999, 2002). These signals are normally derived from visual inputs, proprioceptive signals and, it is thought, from efferent signals commanding new actions. Without proprioception, deafferented subjects are very reliant on vision, and can show near normal performance in visual tasks such as joystick-tracking or visual reaching. However, they show very impaired performance in tasks performed without continuous visual information. It is still a moot point whether they have access to reliable efferent signals (Farrer et al. 2003; Fourneret et al. 2002).

There can, of course, be situations where the signals from vision and proprioception conflict, for example when using prismatic or inverting lenses, or more commonly when using a mirror. Here visual cues about the visual target are mirror reversed with respect to the hand motion. This conflict between vision and proprioception can cause difficulties, and guiding visual actions in a mirror takes considerable practice. It was therefore interesting that a deafferented subject, GL, was found to have significantly better performance than control subjects in a mirror drawing task, and that the control subjects took time to approach her level of performance, which was quite stable (Lajoie et al. 1992). The authors argued that, since GL lacks proprioception, her performance advantage was because she has no visual-proprioceptive conflict to overcome (Lajoie et al. 1992). In support of this, Balslev et al. (2004) recently showed that reducing somatosensory function in control subjects with repetitive transcranial magnetic stimulation simultaneously reduced proprioception and increased the speed of circle-tracing with a mirror-reversed cursor.

However, it is still surprising that GL did not experience any difficulty in performing the mirror drawing task. She would have been subject to the same planning conflict between using mirror-reversed visual cues instructing the direction to move and directing hand actions in the opposite direction. For example, when looking in the mirror, a line that is shown running towards the top left must be followed by a pen movement either towards the bottom left or the top right, depending on the placement of the mirror. Thus even without proprioception, planning in which direction to move next is made difficult by the mirror reversal. As these planning conflicts are most pronounced when there are sharp changes of direction, at corners in the shape being followed (Tsao 1950; Scheidemann 1950), we therefore aimed to test control subjects and another deafferented subject in a similar mirror-tracing task, in which we could manipulate the amount of conflict between vision and action, by varying the complexity of the shapes to be traced. We hypothesize that mirror-tracing of shapes with complex corners should present difficulties to both control subjects and the deafferented man. Tracing smooth curved templates that do not have sharp corner points may then expose an underlying visuo-proprioceptive conflict in the control group only, as Lajoie et al. (1992) have reported in their contrast between GL and control subjects, albeit tracing a Star of David template.

Methods

Subjects

We tested IW, a 53-year-old left-handed man who had suffered a peripheral deafferentation some 30 years previously. IW has been studied extensively and detailed reports on his proprioceptive loss are available (Cole 1995, 1998; Cole and Sedgwick 1992; Cole et al. 1995). He has achieved no neurological recovery. While he has spared perceptions of muscle fatigue, pain and temperature, though with some reduced A-delta and C fibre function, he has no sense of touch, and no perception of joint motion or position. He has no large myelinated fibre afferent input, as assessed by clinical neurophysiological measures (no sensory nerve conduction and no sensory or motor reflex activity (Cole 1995, 1998; Cole and Paillard 1995; Cole and Katifi 1991).

We also tested six control subjects (mean age 51 years ± SEM 3, range 40–57), including the two authors. One of the controls was left-handed. All subjects gave informed consent, and the experiments were performed under local ethical guidance.

Task

Subjects were instructed to use their preferred hand to hold a pen: a Polhemus digitising stylus, the sharp tip of which had been replaced with a smoothed wooden cone. This provided a drawing instrument that had the feel of a blunt pencil, but left no mark on the paper. Its position was registered at 120 Hz with precision of less than 1 mm.

The subjects sat in front of a semi-silvered front-surfaced mirror (Fig. 1a) and at the start of each trial placed the pen tip on a 5 mm black dot on the paper surface. When ready, an occluding cardboard sheet was removed from the distal side of the mirror, revealing a template shape that they were to trace. The start position of the template seen through the mirror was spatially aligned with the virtual images of the starting dot and pen tip, reflected in the mirror. Subjects then immediately traced the template, under instruction to move as fast and accurately as possible, attempting to stay within the template's lines. At the end of the line they lifted the pen away from the paper, providing a clear mark of the end of their tracing action.

Twelve templates were used, consisting of six pairs of templates that were mirror images of each other (Fig. 1b). Five of these were straight-line shapes with horizontal and oblique lines, with 2, 4, 6, 8 and 10 corners, respectively. The sixth shape was a smoothed curve. All templates had a total line length of 22 cm and a line width of 6.6 mm. Templates were presented in pseudorandom order, balanced across control subjects, with four repetitions of the six basic shapes (24 trials). For the deafferented subject, we presented the curved shapes 8 times, giving a total of 28 trials.

Analysis

The digitised tracing movements were analysed in Matlab. The movement duration and total drawn line length were recorded for each trial and averaged across the repetitions of each of the six shapes. For the control subjects, group averages were then calculated. Tracing error was quantified as the mean distance of the pen-tip from the nearest point of the template,

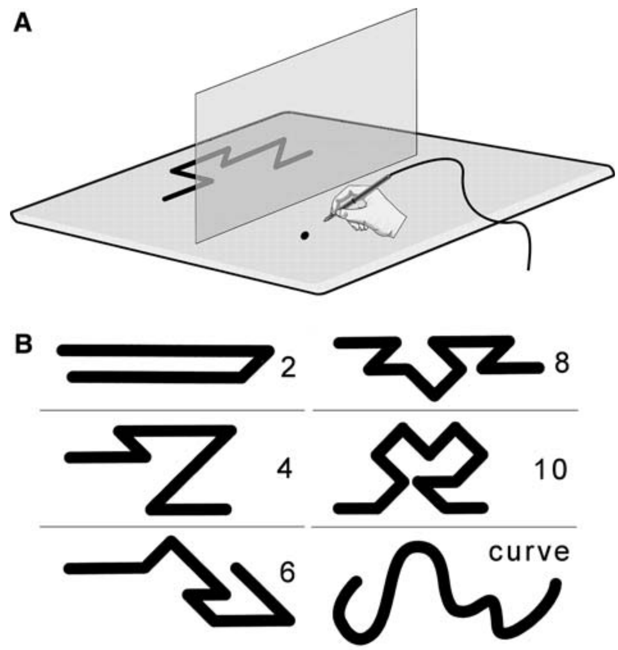

Fig. 1 **a** Experimental set up. The subject sat in front of semi-silvered mirror, viewing a template through the glass, and tracing the shape with the pen, reflected in the mirror. In the orientation of this figure, the subject sat to the right of the mirror, as a comfortable position to see target and the reflected image of the hand, and to draw on the digitizing tablet. **b** The six templates used. During testing, each was presented as shown, as well as in its top–bottom mirrored form. Subjects always started from the left end of each shape

across all data samples. Hence error was zero if the pen was inside the 6.6 mm wide template.

To assess practice effects, we also averaged movement durations across four sequential blocks of 6 (or 7) trials, each including all the template shapes.

We then measured power spectral density curves, in order to assess the smoothness of each traced line. The pen tip velocity was first calculated separately for vertical and horizontal axes, zero-meaned and Hanning filtered before two power spectra were calculated, one for each axis, and averaged together. Spectra were then averaged across all repetitions of each of the six template shapes, and the subject-averaged spectra were smoothed with a Gaussian filter (FWHM 8 data points, 0.28 Hz). Group mean spectra for the controls were calculated after smoothing.

Results

Tracing linear templates

All control subjects showed difficulty in performing the mirror tracing task; they were relatively fast at the horizontal (left–right) segments, which were unaffected by the top–bottom mirror reversal, but they often showed great difficulty when tracing the oblique segments (Fig. 2a). All subjects were able to complete the simpler figures, with fewer corners, more rapidly than the complex shapes. Thus there was a strong linear relationship between the average tracing time and the number of corners (solid line, Fig. 3a). However, all subjects also showed rapid improvement in performance, and the average movement duration in the fourth block of trials was only 64% of that in the first block (Fig. 3b).

The deafferented subject showed similar patterns of tracing performance (Fig. 2b). On average his movements were 14% faster than that of the controls when tracing the linear shapes (dashed line, Fig. 3a). However, his movement durations were only just outside the 1 SEM intervals for the control subjects: a mixed 2 (subject: IW or control) × 6 (shape) ANOVA showed a significant effect of shape [$F(5,25) = 12.18$, $P < 0.0001$] but no effect of subject group ($P = 0.71$) or group–shape interaction ($P = 0.87$). Although we did not formally test IW's performance in a direct drawing condition, we did ask him at the end of the experiment to trace once around the 2 and 10 corner shapes, as well as the curved shape, directly onto the paper. The average duration of these three trials is shown in Fig. 3a (square, error bar indicates range), and is considerably smaller than his average duration in the six mirror conditions ($t = 4.52$, $df = 5$, $P = 0.006$, 2-tailed one-sample t-test). Hence his performance is significantly affected by having to use the mirror. IW also showed a rapid improvement in performance with practice of the mirror condition (Fig. 3b), such that his movement durations in the fourth block of trials were only 47% of those in the first block (Fig. 3a). Again, a mixed 2 (subject: IW or control) × 4 (block) ANOVA showed a significant effect of block ($F(3,15) = 6.26$, $P < 0.006$) but no effect of subject group ($P = 0.75$) or group–shape interaction ($P = 0.90$).

The slightly higher movement speeds shown by IW might have reflected a speed-accuracy trade-off. However, his mean accuracy was quite consistent across the six different shapes (Fig. 4a), and was higher than the mean control group accuracy ($t = 5.96$, $P = 0.002$, 2-tailed one-sample t-test). Furthermore, his mean drawn line–length across all six shapes (Fig. 4b) was not significantly different than the controls ($t = 0.77$, $P = 0.47$), which indicates that his shorter movement duration was not due to a reduced drawing length.

To estimate the relative time of tracing the linear segments versus the corners, extrapolation of regression lines fitted to data in Fig. 3a, using the results from

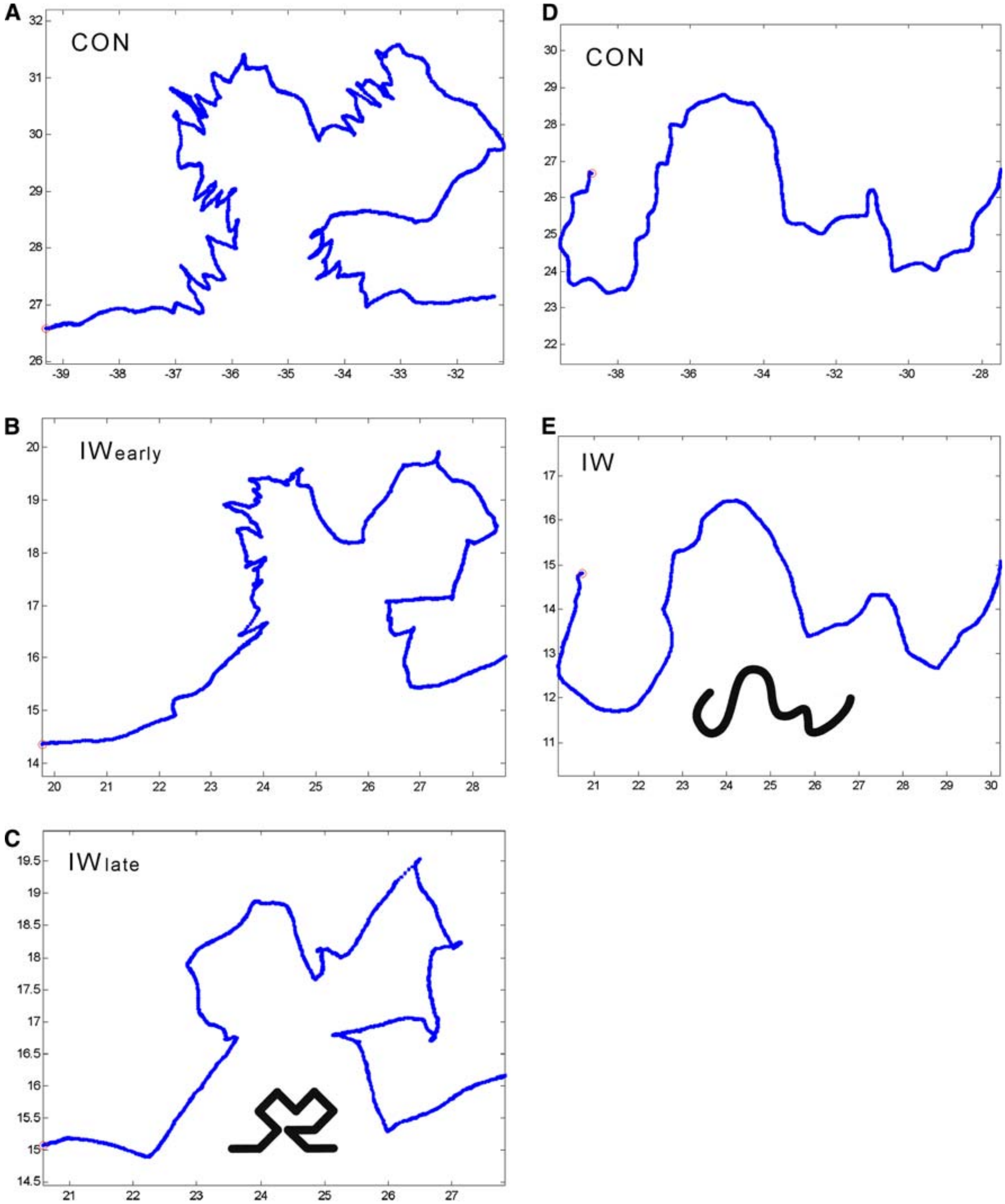

Fig. 2 **a**–**c**Typical examples of tracing the most complex corner-shape. **a** A typical control subject's tracing of a 10 corner template. This is this subject's ninth trial, and his second tracing of a 10-corner template. **b** IW's seventh trial, and his second tracing of this shape. **c** IW's 21st trial, his 4th tracing of a 10-corner template; the inset shows the template, at one quarter scale. **d, e** Typical examples of tracing the curved template. **d** The 15th trial for the same control subject shown in *panel A*. This is his third tracing of the curved shape. **e** IW's 13th trial, and his 4th tracing of the curve; the inset shows the template, at one-quarter scale

templates with 2–10 corners, suggests that the drawing time for a shape without corners would have been 7.0 s (± SE = 2.4 s) for the controls, and 4.1 s (± 2.8 s) for subject IW. For the control subjects, the average time penalty was 1.88 s (± 0.36 s) per corner and this increased to 2.05 s (± 0.42 s) for IW.

Tracing curved shapes

All subjects found tracing the curved templates relatively easy, and their movement durations reflected this (Fig. 3a). The pen movements were also much more controlled (Fig. 2d), showing smaller deviations

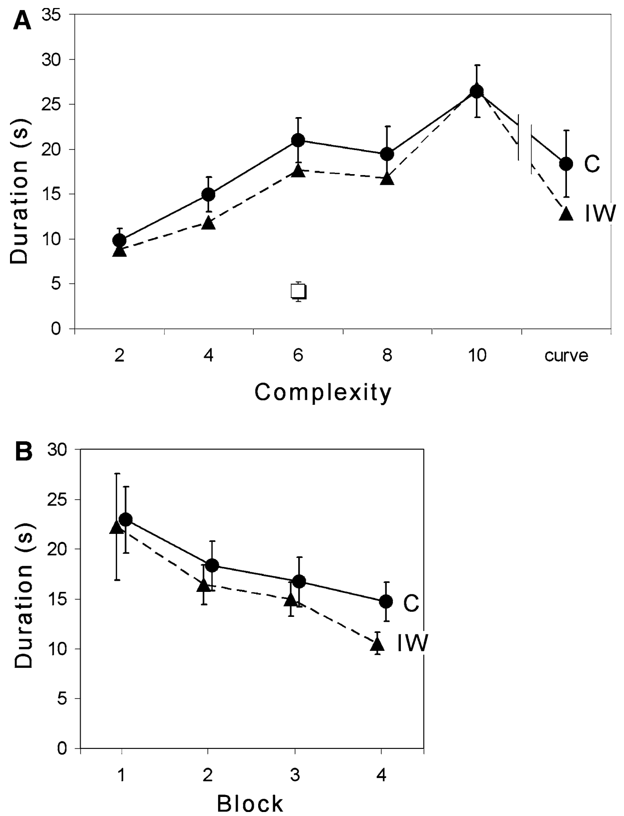

Fig. 3 Mean drawing durations. **a** Movement durations were averaged across all repetitions of the six template shapes, with 2–10 corners or continuous curves. **b** Effect of practice. Movement durations were averaged across four successive blocks of trials, including all template shapes. Subject IW's within-shape average data are compared with the within-group average control data (*C*, ± 1 SEM). The *square symbol* (**a**) is the mean (*error bar* = range) for three trials in which IW directly traced the templates, without the mirror. One trial each was recorded for the curved, 2 and 10 corner templates

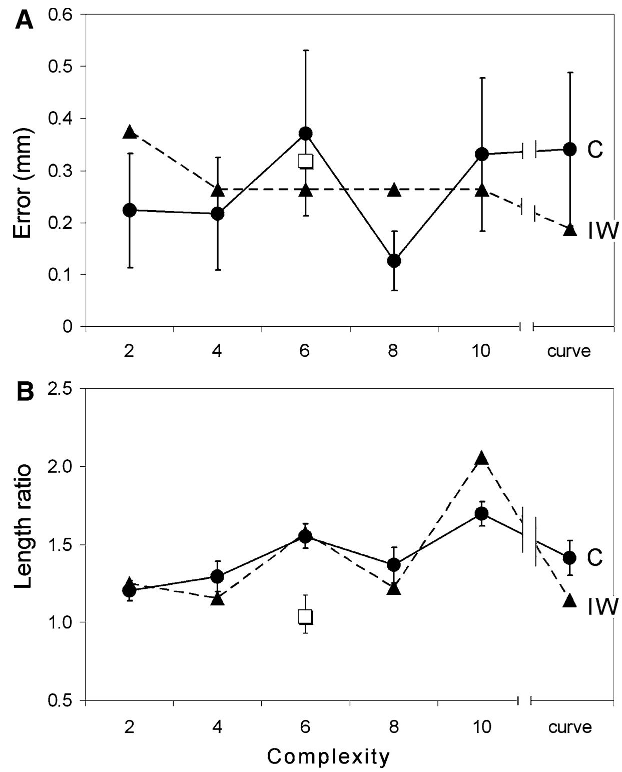

Fig. 4 Mean drawing accuracy. **a** Pen movement accuracy averaged across all repetitions of the six template shapes, with 2–10 corners or with continuous curves. **b** Mean drawn line-length as a ratio of template length. For both panels, subject IW's within-shape average data are compared with the within-group average control data (*C*, ± 1 SEM). The *square symbol* is for 3 direct vision trials (see Fig. 2a)

from the template, and far less "hunting" (Fig. 4b, compare Fig. 2a, d). However, the control subjects followed the curved trajectory in an average of 18.3 s, which is 2.6 times slower than predicted by the regression analysis for a straight line, despite the lack of sharp corners. Hence even these curved templates do impose a time–cost for the controls. In contrast, subject IW was particularly smooth and fast when tracing the curved templates (Fig. 2e), with an average duration of only 12.8 s. Hence his curve drawing movement durations were 46% faster than the controls. The relative duration for him to complete the curve tracing, compared to his performance on the 2-corner shape (which was chosen as the shape with least corners) was significantly reduced compared to the controls ($t = 2.28$, $P = 0.035$). His mean accuracy when drawing the curved shapes was also good, in comparison to the controls (Fig. 4). Again, this rules out an increase in speed at the expense of accuracy.

The increase in speed and smoothness demonstrated by IW for the curve tracing was reflected in the power spectra (Fig. 5, bottom right), in which the amount of power at frequencies of between 1 and 2 Hz reflects the intermittent visually guided corrections in pen motion (Miall et al. 1993). The difference between intermittency in the linear and curves templates is most marked for IW, who shows a steep monotonic decline in power across the frequency range only when tracing the curved template. In contrast, in all other conditions for IW, and in all conditions for the control group, there is a noticeable shoulder in the power spectrum at about 1.5–2.0 Hz (Fig. 5).

Discussion

The aim of this study was to extend the findings of Lajoie et al. (1992), based on mirror tracing of a single star-shaped template by the deafferented woman GL, in order to test the effects of changes in template complexity. She did not show any delay in mirror drawing,

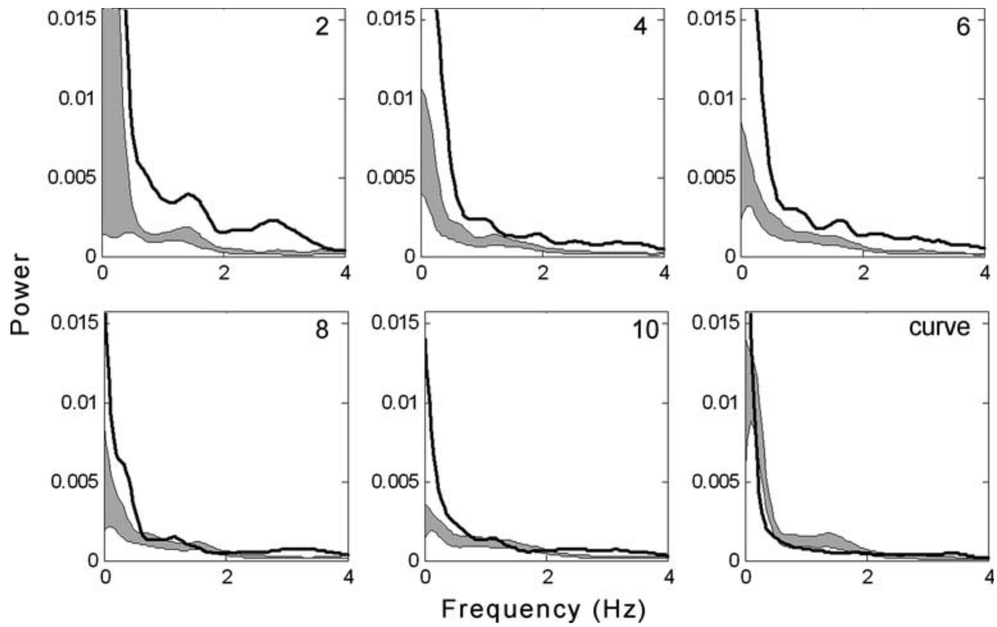

Fig. 5 Mean power spectra calculated for tracing around the curved template shapes. Control data are indicated by the *grey zone*, ± 1 SEM around the group mean. The average power spectrum for subject IW is shown by the *heavy black lines*. Note the shoulder in the power curves at approx 1.5–2.0 Hz that is present for the controls in all spectra, but is absent in IW's data for the curve condition

and had no learning effect, a result suggested to be due to her using on-line visual processing to guide movement rather than her using forward motor planning. In everyday life and in contrast to GL, however, the similarly deafferented man IW does show evidence of such planning (Cole 1995; Ingram et al. 2000) and so we hypothesised that his performance would be closer to that of controls.

In addition, because we hypothesize that forward planning of actions would be confounded by the mirror-reversal of visual cues, we expected that any difference in performance between controls and IW would depend on the complexity of the template, which in turn reflected the complexity of conflict between visual cues and motor plans. Thus, we hypothesized that IW's performance would show an increased duration to trace around complex, multi-cornered shapes that require forward planning, compared to simpler templates that might be followed using visual feedback.

The subject IW has been well documented previously, and has very limited sensation from his limbs (Cole 1995; Cole and Katifi 1991). These remaining afferent signals would not be expected to contribute to his performance when mirror drawing, and he may be considered to use only visual control for this task (Ingram et al. 2000; Blouin et al. 1996). The most striking finding was that IW was very close to normal in the majority of his mirror-tracing performance, showing nearly the same pattern of increasing movement duration with template complexity, and showing as great—if not slightly greater—effects of practice. Both results contradict those of Lajoie et al. (1992), testing deafferented subject GL. However, when we tested IW on continuously curved templates, he was significantly faster than the controls, and the relative duration for drawing the curves compared to the simplest, 2-corner, shape was significantly reduced. His movements, as assessed by frequency analysis, were much smoother, and his accuracy higher. Hence his performance in the curve-tracing condition was more similar to that predicted by Lajoie et al. (1992), albeit in drawing around a Star of David shape with 6 acute corners.

The linear increase in movement duration seen with the number of corners in the templates argues that the main time–penalty is due to the sharp changes in movement direction at each corner. As the templates were all of equal length, we cannot directly measure the cost of drawing straight lines, which we did not include in our test set. However, regression analysis suggested that IW would be faster on the straight than controls, and this increased movement speed has been seen in other point to point movement tasks (Ingram et al. 2000). It is possible that his extensive practice over 30 years of controlling his limbs using only visual feedback has allowed him to use visual control of movement more rapidly than control subjects. Alternatively, his movements may be faster because he does not need to wait on feedback from proprioception (Ingram et al. 2000). IW also suffered a time penalty per corner, but this appears of approximately equal magnitude to the controls. It is thus significant that IW was significantly faster than the control group when following the curved lines.

Our results therefore suggest that Lajoie's argument (1992), that deafferentation released GL from a purely visuo-proprioceptive conflict, cannot easily be applied to IW. For him, there is as much difficulty in performing the mirror task as for control subjects, with a planning cost per corner as high as that of the controls. He also shows similar or greater improvement over time than the controls. Thus unlike subject GL, IW does suffer a conflict when tracing in a mirror and—without proprioception—this must represent a conflict between vision and action commands: a visuo-motor conflict instead of a visuo-proprioceptive conflict. IW claims to think and plan out each action, using vision to supervise the accuracy of these movements. In these circumstances, the mirror reversal between the visual goal and the required pen movement is difficult. The difference in performance between the two deafferented subjects suggests that GL is more biased towards use of on-line visual feedback and less towards forward motor planning than is subject IW.

Why then is IW significantly better at the curved templates than the controls? One possibility is that following a line (whether it be the straight segment between corners of the linear shapes, or the gentle curves of the curved template) releases him from explicit planning, and invokes some more "on-line" control process. We expect this shift between feedforward and feedback control to be a bias, rather than all-or-none.

Hence it may be that between corners, or when the curves are gentle, the control subjects are still handicapped by a visuo-proprioceptive conflict, as Lajoie et al. (1992) suggested, and IW is not. Previous work (Balslev et al. 2004) is consistent with this—reducing proprioceptive function by rTMS over somatosensory cortex in normal subjects improved their mirror-tracking of circles. Balslev et al. (2004) did not test complex templates, but did see a similar effect in simple point to point movements (personal communication).

The proposed shift from visually based planning towards greater on-line, visual feedback control of actions is consistent with recent unpublished work by Dawson and colleagues (Rosenbaum et al. 2006). They have shown that haptic tracking appears to involve no high level planning, such that the two hands can simultaneously follow different trajectories. This is not possible if subjects follow visual paths, and Rosenbaum et al. (2006) argue that tracking a visual path requires a visuo-motor planning stage.

In summary, the conflict experience when mirror-drawing is not only, we believe, between mirror-reversed vision and proprioception (1992), but also between vision and planned actions. This is in agreement with multi-process models of adaptation to movement under conditions with prism-lens perturbed visual feedback that emphasize changes in the strategic control of movement that occur concurrent with a process of visuo-proprioceptive recalibration (Redding et al. 2005). One reason for IW's success in rehabilitation after deafferentation, allowing him to walk and live independently, may lie in his ability to elaborate and use these strategic motor plans.

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