Brain Research Bulletin 79 (2009) 365–370

Contents lists available at ScienceDirect

Brain Research Bulletin

journal homepage: www.elsevier.com/locate/brainresbull

Research report

Role of proprioception and vision in handwriting

Marie-Claude Hepp-Reymond[a], Vihren Chakarov[b,c], Jürgen Schulte-Mönting[d], Frank Huethe[b], Rumyana Kristeva[b,*]

[a] Institute of Neuroinformatics, University of Zurich and ETH Zurich, Switzerland
[b] Neurological Clinic, Albert-Ludwigs University of Freiburg, Breisacherstraße 64, 79106 Freiburg, Germany
[c] Centre of Biomedical Engineering, Bulgarian Academy of Sciences, Sofia, Bulgaria
[d] Department of Biometry, University of Freiburg, Germany

ARTICLE INFO

Article history:
Received 13 November 2008
Received in revised form 7 May 2009
Accepted 7 May 2009
Available online 20 May 2009

Keywords:
Motor control
Handwriting
Deafferentation
Proprioception
Vision
Feedback

ABSTRACT

The objective of this study is to better understand the role of proprioception in handwriting and test earlier conclusions stating that the automated shaping of letters was not impaired by the removal of visual control in deafferentation. To this aim we compared the performance of the deafferented patient GL, who suffers from a complete loss of cutaneous and proprioceptive sensation, with that of eight healthy age- and sex-matched subjects. The word "Parallele", written within a short sentence with and without visual control, was quantified using a digital writing tablet. Three of the 13 analyzed parameters were strikingly different in patient GL compared to healthy subjects, both *with* and *without* vision: increase of number of pen touches, increase in number of inversions in velocity, and decrease of mean stroke frequency. The changes in these three parameters indicate a strong impairment in automated behaviour in the absence of proprioception and touch. This impairment is also supported by the significantly longer movement duration, which is also significantly increased by the removal of visual control.

The present study provides for the first time a quantification of handwriting in a completely deafferented patient and reveals the central role of proprioception for the storage, updating, and maintenance of skilled motor programs. The fact that the deficits are already present with visual feedback suggests that the role of vision in handwriting is only secondary.

1. Introduction

The relative role of vision and proprioception in the generation and control of fine complex motor skills has been the object of many studies, mainly focusing on reaching and grasping. Persons with experimentally induced sensibility deficits and patients suffering from severe polysensory neuropathies or strokes are impaired in using their hands when controlling force and in fine manipulations [22,28,8,11,5,12,24,46,6,13]. These investigations strongly suggest that cutaneous and proprioceptive feedback are absolutely necessary for updating motor memories and internal models whereas visual information, providing feedforward information, may in a predictive mode only adjust the motor commands [8,29,2].

One important highly complex daily motor skill is handwriting. A first requirement for writing is the coordination of multiple joints in the hand, wrist, elbow, and shoulder to form letters, numbers, and symbols, and to place them in space [14,15]. Second, to hold a pen and guide it on a paper relies mostly on sensory signals from skin, joints and muscles of the hand, providing adaptation to the pen–paper friction [37,3,46]. Finally, most handwriting activities, trained and improved over years, are highly automated, calling on motor programs stored in motor memory [21,41,47,4]. They may be far less dependent on a moment-to-moment visual guidance than other complex movements as they are characterized as open-loop performance, with bell-shaped velocity curves and little attentive guidance [19].

The question of the role of vision in handwriting has been specifically addressed in healthy subjects by several groups [35,34,45,42,43,17,18]. However, no general consensus has been reached so far as, depending on the experimental conditions, the removal of vision induced increase in movement time and size of trajectories [35,43], or modifications in the production of strokes and letters [45], or no clear deficits at all, unless vision and attention were manipulated [17,18].

With respect to the role of proprioception, deficits in handwriting after pathological deafferentation have been up to now described only for two patients. Rothwell et al. [26] investigated the manual performance of the patient GO who suffered from strong sensory deficits in arms and hands, legs, and feet. The loss concerned mainly pinprick sensation, vibration, and light touch. In this

* Corresponding author. Tel.: +49 761 270 5411; fax: +49 761 270 5416.
E-mail address: rumyana.kristeva@uniklinik-freiburg.de (R. Kristeva).
URL: http://www.uniklinik-freiburg.de/neurologie/live/forschung/xpeeg.html (R. Kristeva).

0361-9230/$ – see front matter © 2009 Elsevier Inc. All rights reserved.
doi:10.1016/j.brainresbull.2009.05.013

patient, though incomplete deafferentation, the deficits were quite severe and his handwriting was unreadable. In another more complete deafferented patient (GL), lacking touch and proprioception up to the level of the nose, Teasdale et al. [36] only found spatial disorganization of the writing when GL had the eyes closed, whereas the letters were normally shaped and recognizable. These observations supported the hypothesis that the automated letter shaping components are preserved in the absence of both proprioceptive and visual feedbacks. This claim, however, can be questioned in view of Ghez and co-workers' findings in patients with large-fiber sensory neuropathy that the control of multijoint movements, such as reaching, requires proprioception [8,9,27]. Although reaching involves the coordination of proximal joints, the question can be raised whether the complex coordination of multiple distal joints, as needed in handwriting, should not also be dependent on an intact proprioception.

To our knowledge, a new analysis of handwriting in deafferented patients is lacking, although many data have been recently reported for several patients in various reaching, weight estimation, and other tasks [20,23,2]. With respect to patient GL, she can grasp and reach nearly normally [1,33,29] and produce and estimate manifolds of force, even without visual feedback [16]. The outcome of these investigations suggests that handwriting features may be preserved thanks to their internal representation and do not need proprioceptive feedback, despite the findings of Ghez and co-workers supporting the opposite interpretation.

The existence of tools, such as pressure-sensitive digitizing boards and specialized software providing a quantification of many handwriting parameters [17], allows precise evaluation of the impairments due to lack of cutaneous sense and proprioception, and of the influence of vision on this skilled performance. Therefore, we investigated the handwriting of the deafferented patient GL with and without visual control, using a digitizing board, and compared her results to those of eight healthy age- and sex-matched subjects. We expected that deficits in letter production under visual control, if any, should be identified and that removal of visual feedback would strongly enhance them.

2. Material and methods

2.1. Subjects

The deafferented patient GL, a right-handed 56-year-old woman participated in the study (for detailed clinical description, see Ref. [7]; http://deafferented.apinc.org//). In brief, after two episodes of extensive sensory polyneuropathy (at the age of 27 and 31) the patient has been suffering from a strong sensory impairment on the whole body up to below the nose, due to affected large diameter peripheral sensory myelinated fibres. The impairment was documented by sural biopsy. The patient has a total loss of touch, vibration, pressure and kinaesthetic senses, and no tendon reflexes in the four limbs. Pain and temperature sensations are still present. The motor fibres are not affected and, as patient GL has no motor deficits, she can perform complex motor tasks and write under visual guidance.

Eight healthy right-handed female subjects (mean age 54.5 ± 3 years), without any history of neurological disease, participated in the study as age- and gender-matched controls. The handedness of patient and controls was tested according to the Oldfield questionnaire [25].

All subjects participated according to the declaration of Helsinki, with informed consent and with the approval of the local ethics committee.

2.2. Experimental paradigm

During the experimental session subjects and patient were sitting in a chair in an electrically shielded, dimly lit room. Their dominant right hand and arm were supported in a rigid cast and the wrist was free to move. The digital board was fixed to the chair in an adjustable way and positioned in the most comfortable way for each subject. For patient GL, the arm was additionally immobilized by strips and the non-inking pen fixed with tape between her thumb and index finger, in the position she generally holds a pen.

The experimental paradigm consisted in writing a test sentence on a digital board with a non-inking pen under two experimental conditions: first with visual control (+VC) and second without (−VC) visual control. For GL who is French speaking the sentence was: "Une Parallele Canada Europe" and for the control subjects who were German speaking "Die Parallele Canada Europa". For each condition the task consisted in writing the sentence repeatedly with a short pause (5 s) between the repetitions, six times for GL in order to avoid fatigue and twenty times for the control subjects. The +VC condition always preceded the −VC, with a 5 min interruption between both.

During the +VC condition the subjects had to look at a 17′ PC monitor reproducing the pen trace. The monitor was at a distance of 1 m in front of the subjects and centred at the eye level. During the (−VC) trials the PC monitor was switched off and the subjects had to fix their gaze on a green dot fixed in the centre of the screen. The hand was in the same posture in both conditions and was hidden by a solid construction that did not disturb the handwriting movements. Thus, the subjects could see neither the graphic table nor their writing hand. Prior to the experiment patient and control subjects had to read the sentence and to write it several times until they felt confident with the task.

The hand of patient GL had to be positioned on the digitizing board before the start of each trial and an experimenter was checking her performance on the board.

2.3. Recordings

The writing performance was recorded using a pressure-sensitive digitizing board (WACOM UD-1212) connected to a PC by 19.200 band serial line and general software package CS Version 4.3 and CSWin 1.0 for the off-line analysis respectively. The position of the writing pen was detected with a sampling frequency of 166 Hz and accuracy 0.2 mm in both X and Y directions. Data were provided when the pen touched the digitizing board or when the pen was lifted above the tablet up to a height of less than 12.7 mm. The maximum recording time was set at 30 s for GL and at 10 s for the controls with rest intervals between trials from 10 to 15 s. This time was the rest period for the subject and was used by the investigator to store the data.

2.4. Writing performance analysis

The software package for calculation of the velocity used non-parametric regression methods (Kernel estimators) that assure extremely small and negligible distortion of the signals (for more details *cf.* [19]).

For each condition the six trials of GL and the first six trials of the controls were taken for the analysis. We selected the same word "Parallelle" from the test sentence, which is easy to segment because it contains many "l" and "e", *i.e.* letters performed in a highly automated way without having to lift the pen from the tablet. The writing performance was estimated by quantifying 13 parameters. Although several measures are not independent from each other, they all represent different aspects of the performance.

The *quality and the level of automaticity* of the handwriting were investigated with the single stroke analysis which is based on handwriting trace decomposition in one-stroke segments, each stroke being defined as single up or down movement of the pen. From a motor control point of view, the strokes are the smallest measurable units of handwriting [39,40]. Following related parameters were measured. First, the mean stroke frequency which gives a measure of the fluency and automaticity of the writing, 4 Hz being a normal predictive mode of motor control and values below 3 Hz indicating impairments [48]. Second, the number of inversions in velocity (NIV), a quantitative evaluation of the inversions of the velocity profile during a single stroke which is equal to 1 when an up or down stroke shows the normal smooth bell-shaped velocity profile as it is in skilled writers and is higher when irregularities occur. And third, the percent of strokes with number of inversions in velocity equal to 1 (NIV = 1) which was calculated from the total number of strokes in the word "Parallele". A high percentage is expected in the open-loop handwriting of healthy subjects.

The *movement duration* was defined as the time between the first and end movement of the word, including: the mean time of pen on paper and mean time of pen in the air. Related to these parameters are the percent of total time of pen on paper and the mean trajectory and absolute velocity of the pen on paper and of pen lifted.

In addition, the number of the pen touches on paper and the mean vertical pressure were also quantified.

2.5. Statistical analysis

On the basis of the mean subjects' values for each writing parameter under the two conditions (+VC and −VC), the statistical significance (set at $p < 0.05$) between patient GL and the healthy controls was assessed for the dependent variables by two-way ANOVAs, with repeated measures of both factors. In this design, the first factor was the between-subjects factor Group (GL and controls) and the second factor was the within-subject factor Mode (−VC and +VC). Note that the ANOVA used by us is a comparison of a single sample with the confidence intervals of the control group. To control the p-values for multiple testing we have in addition performed α-adjustment after Holm for the parameters with significant differences [10].

3. Results

Though her strong proprioceptive and cutaneous deficits, GL managed to write the sentence on the digitizing board, even with-

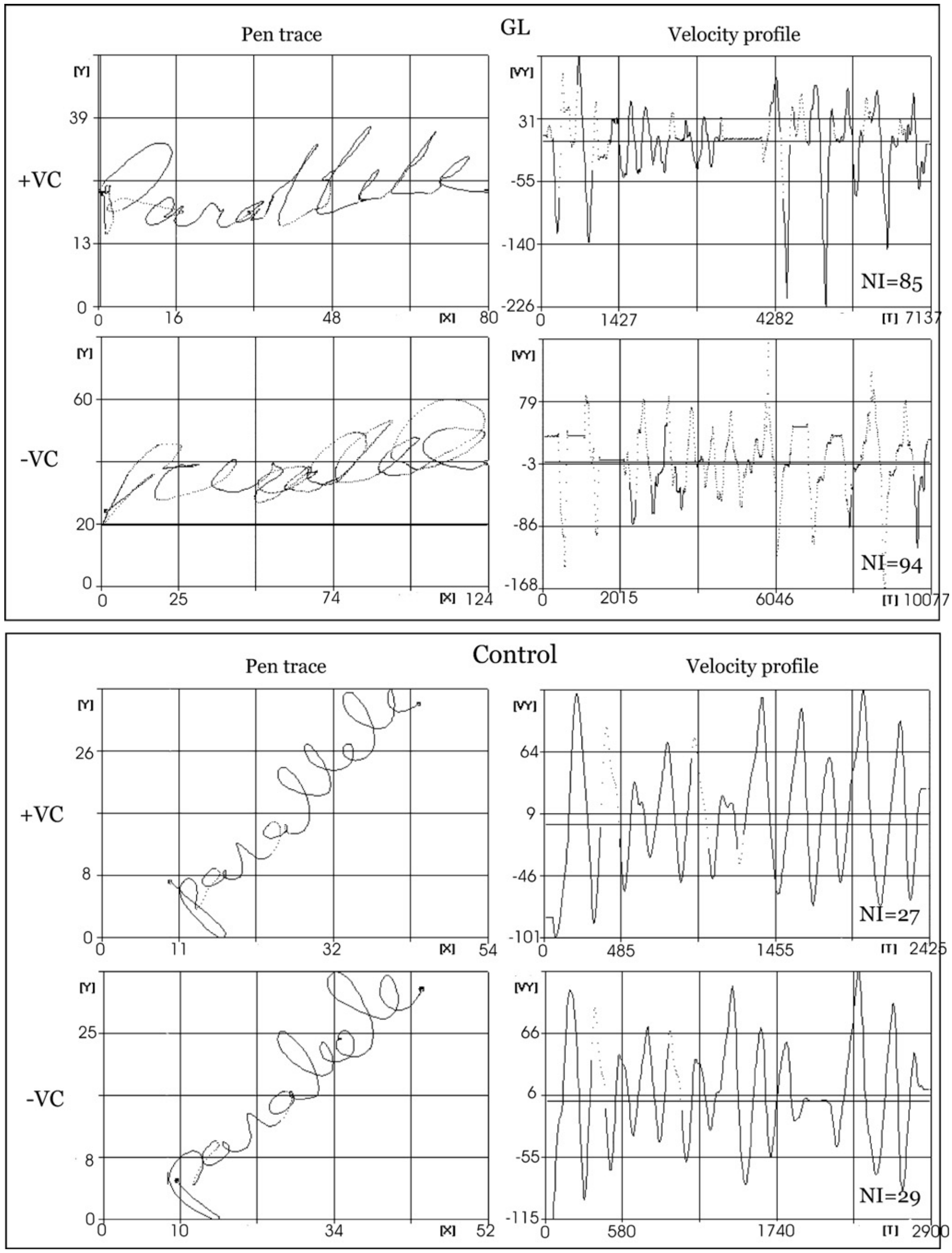

Fig. 1. Original pen traces (left panel) and velocity profiles (right panels) of patient GL (upper part) and one control subject (lower part). The plots on the left represent the *x*/*y* coordinate plot of the tip of the pen on the digitizing tablet (in mm). The plots on the right are the corresponding velocity profiles with time in ms on the *x*-axis (*T*) and velocity on the *y*-axis (*V*, mm/s). Note the longer movement duration and the higher number of inversions in velocity (NI) in patient GL in comparison to the control subject, as well with (+VC) and without visual control (−VC). Note also the longer trajectory pen lifted (dotted line in pen traces and velocity profiles) in patient GL, especially in the −VC condition.

out seeing her hand. She reported at the end of the experiment that she did not know whether the pen still was in her hand and that the handwriting task was not an easy one, especially without visual control. The original pen traces of patient GL and of one control and their corresponding velocity profiles are displayed in Fig. 1 for both conditions, *i.e.* with and without visual control (+VC and −VC respectively).

In Fig. 1 some qualitative differences in writing and velocity profiles are already obvious between patient GL and the control subjects in the + VC condition, especially the longer writing duration, the irregularities in letter shaping, and the higher number of inversions (NI) in GL. In addition, it is apparent that without vision the handwriting of the patient is strongly degraded.

The quantification of the 13 selected handwriting parameters (see Section 2) revealed clearly the impairments of GL. The mean intertrial values and SDs of these parameters are listed for the patient and the eight healthy subjects in Table 1.

The two-way ANOVAs revealed significant main effects for the factor Group (between-subjects, patient and controls), for the factor Mode (within-subject, +VC and −VC), and for both Group and Mode and their interactions. The results of the ANOVAs are shown in Table 2.

This statistical analysis disclosed that for four handwriting parameters both, differences between GL and the controls (factor Group) and between with and without vision (factor Mode) as well as *their interactions* were significant (Table 2). These

Table 1
Mean values and SD for the 13 quantified handwriting parameters. $N = 6$ for the patient GL and $N = 48$ (8×6) for the controls.

Handwriting parameters	+VC		−VC	
	Patient GL	Controls	Patient GL	Controls
Movement duration (ms)	6835 ± 343	2847 ± 387	8746 ± 944	2757 ± 330
Mean time pen on paper (ms)	3736 ± 835	2359 ± 462	4517 ± 2153	2348 ± 372
Mean time pen lifted (ms)	3086 ± 985	484 ± 275	3542 ± 2695	407 ± 188
Percent of total time of pen on paper	55 ± 13	83 ± 10	58 ± 29	85 ± 6
Mean trajectory pen on paper (mm)	201 ± 49	190 ± 54	331 ± 188	210 ± 47
Mean trajectory pen lifted (mm)	103 ± 24	31 ± 23	223 ± 183	28 ± 14
Number of pen touches on paper	11.8 ± 2	4.1 ± 1.5	7 ± 2	4 ± 1
Absolute velocity pen on paper (mm/s)	54 ± 5	82 ± 24	74 ± 20	90 ± 18
Absolute velocity pen lifted (mm/s)	34 ± 4	63 ± 19	66 ± 19	70 ± 15
Mean vertical pressure (N)	0.28 ± 0.1	0.25 ± 0.11	0.24 ± 0.14	0.31 ± 0.13
Mean stroke frequency (Hz)	2.8 ± 0.2	4.6 ± 0.6	1.8 ± 0.4	4.7 ± 0.6
Number of inversions in velocity/stroke	1.8 ± 0.2	1.1 ± 0.1	2.5 ± 1	1.1 ± 0.1
Percent of strokes with NIV = 1	68 ± 14	95 ± 5	54 ± 11	96 ± 4.3

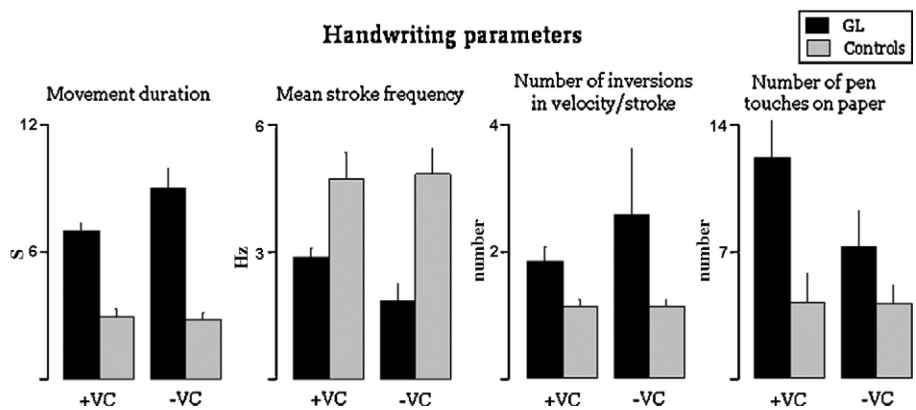

Fig. 2. Mean values and SD for the handwriting parameters of patient GL (black columns) and control group (grey columns) with significant main and interaction effects in the ANOVA analysis. +VC: with visual control; −VC: without visual control.

parameters are displayed graphically in Fig. 2 which clearly shows the longer movement duration (Group $p = 0.0001$, Mode $p = 0.0007$, interaction $p = 0.0002$), higher number of pen touches (Group $p = 0.02$, Mode $p = 0.001$, interaction $p = 0.003$), the lower mean stroke frequency (Group $p = 0.004$, Mode $p = 0.001$, interaction $p = 0.0003$), and the higher number of inversions in velocity (Group $p = 0.0001$, Mode $p = 0.006$, interaction $p = 0.0004$) in the patient. The outcome of the statistical analysis speaks in favor of a clear *impairment of patient GL in writing automaticity.* In addition, the removal of vision further enhanced all these impairments.

Differences between patient and controls (main effect Group) occurred for two temporal parameters as the patient was significantly slower than the controls in both mean time pen on paper (F [1,7] = 9.1, $p = 0.02$) and mean time pen lifted (F [1,7] = 18.7, $p = 0.004$). In addition, the mean trajectory pen lifted *(i.e.* the loss of contact with the digitizing board, see Fig. 1) was also significantly longer in the patient (F [1,7] = 10.0, $p = 0.02$). Finally, the percent of strokes with NIV = 1 was significantly smaller for GL than for the controls (F [1,7] = 66.0, $p < 0.0001$).

The influence of vision alone (main effect Mode) occurred for three parameters specifically affected by its removal. The first one is the mean trajectory on paper (F [1,7] = 5.9, $p = 0.04$) which significantly increased for both GL and controls. This suggests that the absence of visual control impaired the precision in letter shaping. The two other ones were the absolute velocity of pen lifted (F [1,7] = 9.7, $p = 0.02$) and of pen on paper (F [1,7] = 5.7, $p = 0.05$), which without vision showed an increase in GL and in the healthy controls as well (Table 1). This probably reflects some loss of control when vision was removed.

With respect to the mean vertical pressure of the pen on the paper, no significant main effects for both factors were found, nor was any interaction.

4. Discussion

The important new message of our quantitative assessment of handwriting in a deafferented patient is that the shaping of letters and automaticity are strongly impaired. Most of these deficits are already present when patient GL has a visual feedback of her writing performance. In addition, several deficits are enhanced by the removal of this feedback. This clearly demonstrates that proprioception and cutaneous senses are a prerequisite to maintain a learned and automated complex motor behaviour such as writing. This quantitative proof of so-called "morphocinetic" deficits in deafferentation is at variance with Teasdale et al. [36] who based their conclusions on observation only. However, writing impairments similar to the present ones have recently been suggested in an experimental model of deafferentation [6].

The handwriting of the patient was characterized by a strong increase of temporal parameters, *i.e.* the increase of movement duration, of the pen on paper and of the pen in the air. An increase in movement duration has also been reported by Ebied et al. [6] in healthy subjects after infiltrating the median nerve with anesthetics. Slowness has also been described in Parkinson patients [37,38], in writer cramp patients with and without visual feedback [4,48], and for MS patients as an increase of stroke duration [31]. For patient GL, the removal of vision produced a significant increase in the total movement duration only.

Table 2
Results of the ANOVA analysis with significance level for the 13 handwriting parameters.

Handwriting parameters	Factors	*F*	*p*
Movement duration	Group	65.3	0.0001
	Mode	33	0.0007
	Group × Mode	54.7	0.0002
Mean time pen on paper	Group	9.1	0.02
	Mode	1.7	0.2
	Group × Mode	1.4	0.3
Mean time pen lifted	Group	18.7	0.004
	Mode	2.2	0.18
	Group × Mode	0.08	0.8
Percent of total time of pen on paper	Group	4.4	0.07
	Mode	4.9	0.06
	Group × Mode	0.8	0.4
Mean trajectory pen on paper	Group	0.8	0.4
	Mode	5.9	0.04
	Group × Mode	1.6	0.2
Mean trajectory pen lifted	Group	10	0.02
	Mode	3.3	0.1
	Group × Mode	3.5	0.1
Number of pen touches on paper	Group	8.9	0.02
	Mode	26.6	0.001
	Group × Mode	19.9	0.003
Absolute velocity pen on paper	Group	1.9	0.2
	Mode	5.7	0.05
	Group × Mode	1.1	0.33
Absolute velocity pen lifted	Group	2.5	0.15
	Mode	9.7	0.02
	Group × Mode	4.1	0.08
Mean vertical pressure	Group	0.04	0.8
	Mode	0.09	0.7
	Group × Mode	3	0.1
Mean stroke frequency	Group	17.4	0.004
	Mode	29.1	0.001
	Group × Mode	44.2	0.0003
Number of inversions in velocity/stroke	Group	257.2	0.0001
	Mode	34.9	0.006
	Group × Mode	38.9	0.0004
Percent of strokes with NIV = 1	Group	66	0.0001
	Mode	2.9	0.13
	Group × Mode	5.1	0.06

The most important finding of the present study is provided by the strong deficits in a group of three handwriting parameters, *i.e.* the increased number of pen touches on paper, the decreased mean stroke frequency, and the higher number of inversions in velocity. These parameters are describing aspects of letter strokes production and give information on the level of automaticity and fluency of the writing. The patient's impairments, already highly significant when she has a visual control of her handwriting, also increased in the absence of vision. However, the fact that the deficits already exist with visual feedback of the performance suggests that the role of vision in handwriting is only secondary. Several studies on handwriting in healthy subjects came to similar conclusions [35,17,19]. That the cutaneous sensation plays an important role in handwriting has been reported by Ebied at al. [6] who, during transient deafferentation, also observed impaired smoothness and directness. The deficits of the deafferented patient GL which are similar to these transient effects give a strong support to the hypothesis that "morphocinetic" features of handwriting requires intact proprioception and touch, even when visual control is provided.

Many factors could have influenced our results and explain discrepancies between the observations of Teasdale et al. [36] and ours besides methodological differences. Controlling a pen when writing requires complex computations for multijoint coordination and integration of the effecter location and position. These processes need a constant update by proprioception [32]. Thus, we cannot exclude that in GL a slow degradation of her internal handwriting representation might have taken place with time due to a loss of updating mechanisms. This could have caused the impairments in letter shaping, both with and without visual feedback.

In patient GL the removal of the visual feedback had a strong hampering effect on the parameters mentioned above. This finding is not surprising having in mind the study of Sainburg et al. [27] who showed that, without vision of the hand and cursor trace, deafferented patients made typical errors at movement reversals in out-and-back reaching movements on a digitizing board. Marquard et al. [17,18] who investigated the impact of vision on handwriting in healthy subjects found that, similar to our own controls, the removal of visual feedback did not impair handwriting. They however reported that the movements slowed down and the number of inversions increased when subjects were visually tracking the pen tip or making mental tracking during writing. They attributed these impairments to an increase in attention load in these two experimental situations. A similar increase in stroke duration had also been reported in healthy subjects [44] as well as in MS patients writing in a closed-loop condition, *i.e.* monitoring the movements of the pen [31]. We cannot exclude that the increase of GL writing impairments when vision was removed was not partly due to such an increase in attention, as she had to strongly rely on a mental representation of the letters during writing.

A puzzling and unexpected finding is the mean vertical pressure exerted by GL which not only differ from that of the controls but also behaved quite differently without vision, decreasing and not increasing as for the controls. This finding is also at odd with other pathologies, such as in writer's cramp patients who generated in absence of visual feedback an increase in vertical pressure [4,30]. This decrease in vertical pressure may be due to a feedforward postural strategy used by GL to hold the pen that may have been less strong when visual feedback of her performance was removed, as she had to strongly concentrate on her motor memory. The fact that the pen was fixed to the thumb and index finger of GL could also be the origin of the lack of pressure increase occurring in healthy subjects when vision was removed.

In conclusion, our investigation which provides new insight on an automated fine manipulative skill, the handwriting, stresses the fact that the morphological aspects of handwriting need intact proprioception and touch. It also demonstrates that the visual support is not sufficient to counter the profound deficits in central representation of handwriting, probably caused by the long-lasting absence of somatosensory feedback.

Conflict of interest

The authors declare that they have no competing financial interests.

Acknowledgment

Supported by DFG grant (Kr 1392/7-5).

References

[1] C. Bard, Y. Turrell, M. Fleury, N. Teasdale, Y. Lamarre, O. Martin, Deafferentation and pointing with visual double-step perturbations, Exp. Brain Res. 125 (1999) 410–416.
[2] P.M. Bernier, R. Chua, C. Bard, I.M. Franks, Updating of an internal model without proprioception: a deafferentation study, Neuroreport 17 (2006) 1421–1425.
[3] G. Cadoret, A.M. Smith, Friction, not texture, dictates grip forces used during object manipulation, J. Neurophysiol. 75 (1996) 1963–1969.

[4] V. Chakarov, S. Hummel, F. Losch, J. Schulte-Mönting, R. Kristeva, Handwriting performance in the absence of visual control in writer's cramp patients: initial observations, BMC Neurol. 6 (2006) 14.
[5] R.M. Dannenbaum, L.A. Jones, The assessment and treatment of patients who have sensory loss following cortical lesions, J. Hand Ther. 6 (1993) 130–138.
[6] A.M. Ebied, G.J. Kemp, S.P. Frostick, The role of cutaneous sensation in the motor function of the hand, J. Orthop. Res. 22 (2004) 862–866.
[7] R. Forget, Y. Lamarre, Rapid elbow flexon in the absence of proprioceptive and cutaneous feedback, Hum. Neurobiol. 6 (1987) 27–37.
[8] C. Ghez, J. Gordon, M.F. Ghilardi, C.N. Christakos, S.E. Cooper, Roles of proprioceptive input in the programming of arm trajectories, Cold Spring Harb. Symp. Quant. Biol. 55 (1990) 837–847.
[9] C. Ghez, J. Gordon, M.F. Ghilardi, Impairments of reaching movements in patients without proprioception. II. Effects of visual information on accuracy, J. Neurophysiol. 73 (1995) 361–372.
[10] M. Holm, R. Vollandt, Multiple Tests und Auswahlverfahren, G. Fischer, Stuttgart, Jena, New York, 1995.
[11] R.S. Johansson, K.J. Cole, Sensory-motor coordination during grasping and manipulative actions, Curr. Opin. Neurobiol. 2 (1992) 815–823.
[12] L.A. Jones, Peripheral mechanisms of touch and proprioception, Can. J. Physiol. Pharmacol. 72 (1993) 484–487.
[13] L.A. Jones, E. Piateski, Contributions of tactile feedback from the hand to the perception of force, Exp. Brain Res. 168 (2006) 298–302.
[14] F. Lacquaniti, Central representations of human limb movement as revealed by studies of drawing and handwriting, Trends Neurosci. 12 (1989) 287–291.
[15] F. Lacquaniti, G. Ferrigno, A. Pedotti, J.F. Soechting, C. Terzuolo, Changes in spatial scale in drawing and handwriting: kinematic contributions by proximal and distal joints, J. Neurosci. 7 (1987) 819–828.
[16] G. Lafargue, J. Paillard, Y. Lamarre, A. Sirigu, Production and perception of grip force without proprioception: is there a sense of effort in deafferented subjects? Eur. J. Neurosci. 17 (2003) 2741–2749.
[17] C. Marquardt, W. Gentz, N. Mai, On the role of vision in skilled handwriting, in: M.L. Simner, G.C. Leedham, A.J.W.M. Thomassen (Eds.), Handwriting and Drawing Research, IOS Press, 1996, pp. 87–97.
[18] C. Marquardt, W. Gentz, N. Mai, Visual control of automated handwriting movements, Exp. Brain Res. 128 (1999) 224–228.
[19] C. Marquardt, N. Mai, A computational procedure for movement analysis in handwriting, J. Neurosci. Methods 52 (1994) 39–45.
[20] J. Messier, S. Adamovich, M. Berkinblit, E. Tunik, H. Poizner, Influence of movement speed on accuracy and coordination of reaching movements to memorized targets in three-dimensional space in a deafferented subject, Exp. Brain Res. 150 (4) (2003) 399–416.
[21] R.G.J. Meulenbroek, P. van Galen, The acquisition of skilled handwriting: discontinuous trends in kinematic variables, in: A.M. Colley, J.R. Beech (Eds.), Cognition, and Action in Skilled Behavior, Elsevier, North-Holland, 1988, pp. 273–281.
[22] E. Moberg, The role of cutaneous afferents in position sense, kinaesthesia, and motor function of the hand, Brain 106 (1983) 1–19.
[23] G. Nicolas, V. Marchand-Pauvert, V. Lasserre, C. Guihenneuc-Jovyaux, E. Pierrot-Deseilligny, L. Jami, Perception of non-voluntary brief contractions in normal subjects and in a deafferented patient, Exp. Brain Res. 161 (2005) 166–179.
[24] D.A. Nowak, J. Hermsdörfer, Selective deficits of grip force control during object manipulation in patients with reduced sensibility of the grasping digits, Neurosci. Res. 47 (2003) 65–72.
[25] C. Oldfield, The assessment and analysis of handedness: the Edinburgh inventory, Neuropsychologia 9 (1971) 97–113.
[26] J.C. Rothwell, M.M. Traub, B.L. Day, J.A. Obeso, P.K. Thomas, C.D. Marsden, Manual motor performance in a deafferented man, Brain 105 (1982) 505–542.
[27] R.L. Sainburg, M.F. Ghilardi, H. Poizner, C. Ghez, Control of limb dynamics in normal subjects and patients without proprioception, J. Neurophysiol. 73 (1995) 820–835.
[28] J.N. Sanes, K.H. Mauritz, E.V. Evarts, M.C. Dalakas, A. Chu, Motor deficits in patients with large-fiber sensory neuropathy, Proc. Natl. Acad. Sci. 8 (1984) 979–982.
[29] F.R. Sarlegna, G.M. Gauthier, C. Bourdin, J.L. Vercher, J. Blouin, Internally driven control of reaching movements: a study on a proprioceptively deafferented subject, Brain Res. Bull. 69 (2006) 404–415.
[30] T. Schenk, N. Mai, Is writer's cramp caused by a deficit of sensorimotor integration? Exp. Brain Res. 136 (3) (2001) 321–330.
[31] T. Schenk, E.U. Walther, N. Mai, Closed and open-loop handwriting performance in patients with multiple sclerosis, Eur. J. Neurol. 7 (2000) 269–279.
[32] R. Shadmehr, S.P. Wise, The Computational Neurobiology of Reaching and Pointing. A Foundation for Motor Learning, MIT Press, Cambridge, MA, 2005.
[33] M. Simoneau, J. Paillard, C. Bard, N. Teasdale, O. Martin, M. Fleury, Y. Lamarre, Role of the feedforward command and reafferent information in the coordination of a passing prehension task, Exp. Brain Res. 128 (1999) 236–242.
[34] M.M. Smyth, Visual control of movement patterns and the grammar of action, Acta Psychol. 70 (1989) 259–265.
[35] M.M. Smyth, G. Silvers, Functions of vision in the control of handwriting, Acta Psychol. 65 (1987) 47–64.
[36] N. Teasdale, R. Forget, C. Bard, J. Paillard, M. Fleury, Y. Lamarre, The role of proprioceptive information for the production of isometric forces and for handwriting tasks, Acta Psychol. 82 (1993) 179–191.
[37] H.L. Teulings, J.L. Contreras-Vidal, G.E. Stelmach, C.H. Adler, Parkinsonism reduces coordination of fingers, wrist, and arm in fine motor control, Exp. Neurol. 146 (1999) 159–170.
[38] H.L. Teulings, G.E. Stelmach, Control of stroke size, peak acceleration, and stroke duration in parkinsonian handwriting, Hum. Mov. Sci. 10 (1991) 315–334.
[39] A.J.V.M. Thomassen, G.P. van Galen, Handwriting as a motor task: experimentation, modelling and simulation, in: J.J. Summers (Ed.), Approaches to the Study of Motor Control and Learning, North Holland, Amsterdam, Netherlands, 1992.
[40] O. Tucha, L. Mecklinger, S. Walitza, K.W. Lange, Attention and movement execution during handwriting, Hum. Mov. Sci. 25 (4–5) (2006) 536–552.
[41] R.E. Van der Plaats, G.P. van Galen, Effects of spatial and motor demands in handwriting, J. Mot. Behav. 22 (1990) 361–385.
[42] R.R. Van Doorn, J.P. Keuss, The role of vision in the temporal and spatial control of handwriting, Acta Psychol. 81 (3) (1992) 269–286.
[43] R.R. Van Doorn, J.P. Keuss, Does the production of letter strokes in handwriting benefit from vision? Acta Psychol. 82 (1993) 275–290.
[44] G.P. Van Galen, Effects of phonological and motoric demands in handwriting: evidence for discrete transmission of information, Acta Psychol. 74 (1990) 259–275.
[45] G.P. Van Galen, M.M. Smyth, R.G.J. Meulenbroek, H. Hylkema, The role of short term memory and motor buffer in handwriting under visual and non-visual guidance, in: R. Flamondon, C.Y. Suen, M.L. Simner (Eds.), Computer Recognition and Human Production of Handwriting, World Scientific, Singapore, 1989.
[46] A.G. Witney, A. Wing, J.L. Thonnard, A.M. Smith, The cutaneous contribution to adaptive precision grip, Trends Neurosci. 27 (2004) 637–643.
[47] P. Zesiger, P. Mounoud, C.A. Hauert, Effects of lexicality and trigram frequency on handwriting production in children and adults, Acta Psychol. 82 (1993) 353–365.
[48] K.E. Zeuner, M. Peller, A. Knutzen, I. Holler, A. Münchau, M. Hallett, G. Deuschl, H.R. Siebner, How to assess motor impairment in writer's cramp, Mov. Disord. 22 (2007) 1102–1109.