



Muscular co-contraction covaries with task load to control the flow of motion in fine motor tasks

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Abstract

This study focuses on the relationship between movement-time fluctuations in fine motor tasks and changing levels of muscular co-contraction. Based on a recent neuromotor noise theory, we expected that increased task stress would increase muscular co-contraction and prolong movement times. Ten right-handed adults performed a graphic task, which elicited local movement-time prolongations. In half the trials, a distracting sound was presented as an external stressor. Besides pen-tip kinematics, two estimates of muscular co-contraction were obtained from the surface EMG measurements of eight arm and hand muscles. The results confirm the presumed co-variation of movement time and co-contraction. We conclude that muscular co-contraction forms a strategic means to adapt the flow of motion to central information processing demands.

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1. Introduction

The present study was set up to test a hypothesis derived from the neuromotor noise theory of goal-directed movements by Van Galen and Van Huygevoort (2000). The hypothesis states that in repetitive motor tasks, prolonged movement times resulting from increased task demands or external stressors would be accompanied by increased levels of muscular co-contraction. In earlier research, only indirect evidence for this hypothesis was

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found in simulations of the muscle-force recruitment process (Van Galen and De Jong, 1995) and from higher levels of axial pen force in a high-precision, graphical aiming task (Van Galen and Van Huyevoort, 2000).

Contemporary research shows that modulating the degree of co-contraction of antagonistic muscles may be an efficient strategy to maintain satisfactory levels of end-point accuracy in goal-directed arm movements (Van Galen and De Jong, 1995; Laursen et al., 1998; Gribble et al., 2003). This finding supports the view that containing output variability through the regulation of limb and muscle stiffness may be an important principle underlying the control of the movements of a redundant effector system (Harris and Wolpert, 1998). Moreover, the finding corroborates earlier suggestions regarding the important role of co-contraction and limb stiffness in motor control as made in studies aimed at unraveling the origin of the loss of motor proficiency in the elderly (Seidler et al., 1998), in patients with hemiparetic cerebral palsy (Levin and Dimov, 1997), and in patients with occupational cramps and other work-related upper-extremity disorders (cf. Van Galen et al., 2002).

According to the neuromotor noise theory of limb displacement by Van Galen and Schomaker (1992) and Van Galen and De Jong (1995), the speed and extent of limb displacement are assumed to be determined by classical Newtonian physics, i.e., by the net driving force of all muscles that act upon the limb's mass.¹ The stiffness of the total limb system is defined by the resistance to change as determined by the mass of the system, by the level of co-contraction, and by any friction with the environment that happens to occur. In the theory, it is further assumed that muscle-force production is a stochastic process, which implies that increasing force levels are accompanied by increasing levels of neuromotor noise. In simulations of the muscle-force recruitment process based on these assumptions, Van Galen and De Jong (1995) could demonstrate that increasing levels of movement speed resulted in higher levels of end-point variability because of the larger muscle forces that are needed for higher speeds, just as described by Fitts' Law. At the same time, the model could also explain that higher levels of limb stiffness through co-contraction had beneficial effects upon the signal-to-noise ratio (SNR) of the movement signal, and therefore, upon end-point accuracy of a movement. The latter relationship held as long as the low-pass filtering effect of limb stiffness was greater than the increase of muscle-force variability with higher levels of muscle force. This optimization process was thought to be at the basis of setting the level of agonist–antagonist muscle forces such that an acceptable speed-accuracy trade-off, as given by Fitts' Law, is guaranteed. (For further details of the theory see Van Galen and De Jong, 1995; for a critical review of the force-control hypothesis in motor control, see Ostry and Feldman, 2003).

Van Gemmert and Van Galen (1997) emphasized that the movement speed that people are capable of realizing in motor tasks, reflects the signal-to-noise ratios of the neuromotor signals responsible for motion, where low speeds are associated with low SNRs. SNRs of neuromotor signals do not only depend on the summed effect of the natural frequencies of the involved biophysical processes, like motor-unit recruitment processes, reflex-induced oscillations, and soft-tissue mechanical vibrations, but also on the cognitive processes

¹ In formula $F = ma + \beta v + ks$, where F is the net driving force of the limb, a the limb acceleration, v the limb velocity, s the limb displacement, m the limb mass, β the viscosity of the joint system, and k is the stiffness of the total limb system.

involved in motion planning. These planning processes may be directed at retrieving and preparing the representations of upcoming movement units (cf. Van Galen et al., 1986; Meulenbroek and Van Galen, 1989), specifying the parameters of these representations (Van Galen and Weber, 1998), monitoring ongoing motor performance (Van den Heuvel et al., 1998), and correcting movement production as soon as accuracy demands fail to be met (cf. Thomassen and Van Galen, 1992). Since in many motor tasks motion planning and execution take place simultaneously, the combination of the biophysical and cognitive processes necessitates the application of the low-pass filtering effect of limb stiffness through elevated co-contraction and/or increased friction with the working surface as described above. This may result in local performance-speed decrements as people try to achieve the intended output-accuracy levels that they have set as a goal of their task performance.

From a theoretical point of view, a possible interesting feature of filtering the motor output signal by stiffness and its inherent effect on the gain of the limb system as a whole, is that the continuous flow of motor output is either stretched or condensed in the time domain depending upon the set of physical and psychological stressors acting upon the motor output signal. In many earlier approaches to chronometric variations of human performance, a strict emphasis has been laid on preparatory and central processing of information in the reaction-time phase preceding the start of motor execution proper (Posner, 1978; Posner and Digirolamo, 2000). In those theories, the duration of an individual motor act is simply the outcome of the summation of the duration of all the serial processing stages that are presumed to take place in advance of the start of the move. Few authors, however, have proposed theories that explain how humans regulate the flow of motion *during* motor execution (but see Van Galen and Schomaker, 1992). Summation of time intervals of preparatory processes cannot fully account for the increase of movement time in more complex tasks because the central processes involved typically occur concurrently with the preparation of oncoming movement segments. On the other hand, the idea that movement duration is intentionally and consciously varied to accommodate more demanding central processing is hardly feasible in the light of the very small but consistent prolongations of movement time in more complex motor tasks. For example, the increase of the duration of an individual letter stroke in producing a more complex (e.g. repetitive) sequence of handwriting strokes is in the order of 5 ms, much shorter than the standard error of planned time intervals (Meulenbroek and Van Galen, 1989; Van Galen et al., 1986).

Evaluating the relationship between changing levels of co-contraction of arm muscles and movement-time fluctuations in cursive handwriting was, for various reasons, considered a major experimental challenge. The arm, having many mechanical degrees of freedom at the level of the shoulder, elbow, wrist, and finger joints, has even more motional degrees of freedom at the muscular level. The small-amplitude arm, hand, and finger movements that are produced in handwriting are controlled by a large number of muscles that span both single and multiple joints. The relationship between specific muscle contractions and resulting pen-tip displacements in handwriting is not always intuitively clear, even when the overall muscle geometry is taken into account. For example, depending on the extent to which the index finger is flexed at a particular moment, contraction of muscles that span and cause rotations around the interphalangeal joints of

the index finger, may either induce a flexion or an extension of this digit. Consequently, the relationship between muscle contraction and end-effector displacement is, in principle, underdetermined (for an analysis of such a redundant relationship between the pen-tip displacements in handwriting and multi-joint arm control, see Meulenbroek et al., 1996).

Also, because recording surface EMG of forearm muscles was a technical challenge (among other reasons because maximum voluntary contractions of muscles located in the deep layers of the arm were expected to be difficult to record reliably), we opted for a more *dynamic*, data-driven EMG data-analysis procedure. Rather than a priori determining, which contractions of the arm muscles under study would be responsible for pen-tip displacements into which directions, we used a post-hoc algorithm that revealed which muscles had what (agonistic or antagonistic) role in the accelerative and decelerative phase of each move separately. In addition to keeping track of the identity of the prime movers, we assessed the momentaneous level of co-contraction, both in the amplitude and time domain. Details of this assessment procedure are specified in Section 2.

In sum, the present study was set up to evaluate the extent to which local and global movement-time prolongations in handwriting would co-occur with increased co-contraction levels of muscles in the forearm. For this purpose, we used a handwriting task that was expected to elicit local and global movement-time prolongations due to the complex letter combinations that needed to be produced (see Van Galen et al., 1986) and an external stressor that in earlier research had proved to be effective in this respect (see Van Gemmert and Van Galen, 1998).

2. Method

2.1. Participants

Ten right-handed adults (seven women and three men) volunteered to participate in this study. Their age ranged between 21 and 35 years (mean age: 26). Participants were selected on the basis of using a cursive, connected script as their habitual handwriting style. None of the participants were aware of the aims of the study. All subjects had normal or corrected-to-normal vision. The participants were treated in compliance with the APA ethical standards.

2.2. Apparatus

A white paper strip, held on the tabletop by means of a custom-made holder (see Fig. 1), was used as writing surface. Pen-tip displacements were recorded by means of an Optotrak 3020 (Northern Digital, Waterloo, Canada) 3D motion-tracking system using two infrared emitting diodes (IREDs) that were fixed alongside the barrel of a regular, ballpoint pen (Bouwhuisen et al., 2002). Adhesive, disposable pre-gelled Ag/AgCl surface EMG disc electrodes (diameter 9 mm) were used for the EMG recordings. Surface EMG signals were amplified by means of an EMG-interface module consisting of a custom-made, front-end physiological amplifier. A 16-bits ODAU II system (Northern Digital, Waterloo, Canada)

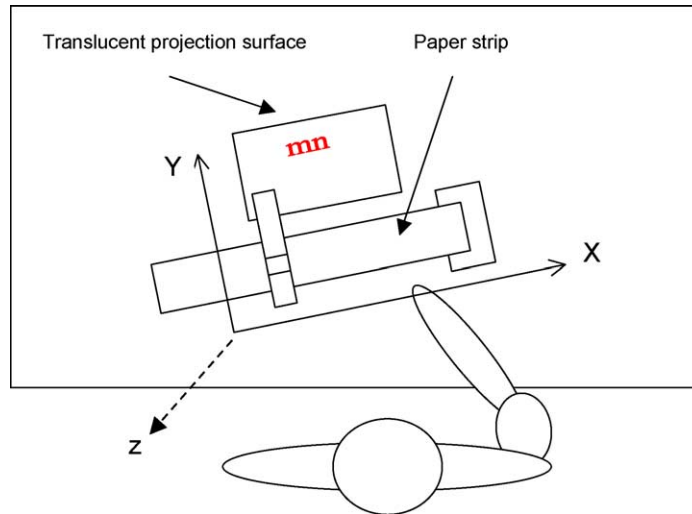


Fig. 1. Experimental set-up and definition of the 3D workspace during the movement recordings. X corresponded to the positive axis running in parallel with the bottom edge of the paper strip, on which participants wrote, Y was defined as the vertical dimension within the writing plane, and Z was defined perpendicular to the writing surface.

was used to synchronize the EMG data collection with the collection of the Optotrak IRED-displacement data. A Pentium-II computer was used for both the data collection and the control of an LCD projector (3 M multimedia projector MP8030), which was used to project the dynamic and static stimuli (see below) onto the writing surface. Headphones (Digital Monitor Stereo Headphones, Monacor, BH-3 ECM) and a sound generator (Thurlby Thunder TG230, 2 MHz, Sweep/Function Generator, RS Components 206-028) were used to present participants with an acoustic distractor consisting of white noise of 75 dB.

2.3. Design

Each participant performed a total of 144 trials divided over four blocks of 36 trials. A single trial lasted 16 s (see Fig. 2). In each trial block, six trial types, making up the letters, n , m , mn , mm , nm , and mn were presented six times each in a random order. The external stressor consisted of a 75 dB white noise acoustic signal, which was counterbalanced across the trial blocks in an ABBA-sequence for five subjects and in a BAAB-sequence for the other five subjects, where A corresponded to the presence and B to the absence of the external stressor. The sound distractor was presented throughout the A-trial blocks.

2.4. The experimental task and predictions

The cursive handwriting task contained features that in earlier studies proved effective in eliciting the movement-time fluctuations that we aimed for (Meulenbroek and Van Galen, 1989; Van Galen et al., 1986; Van Galen and Van Huygevoort, 2000; Van Gemmert

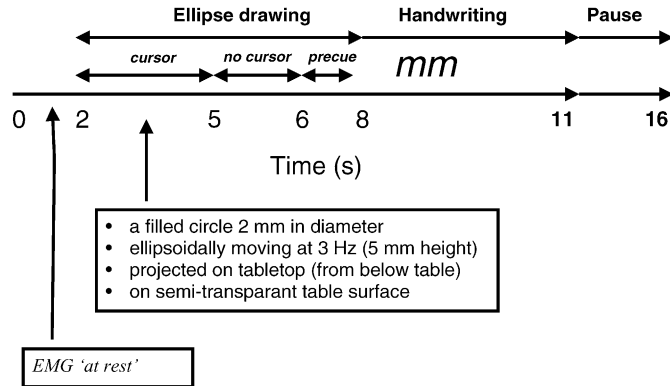


Fig. 2. Sequence of trial events. Between trials, a pause of 5 s was used.

and Van Galen, 1997). Participants were asked to write repeatedly the letter pairs *nn*, *mm*, *nm*, and *mn*. The letters ‘*m*’ and ‘*n*’ were chosen as task letters because to a large extent they consist of pen-tip trajectories that are performed clockwise. Only after the completion of the last down stroke of each of these particular letters does the trajectory change to an anti-clockwise trajectory. This change in direction at the connection between the two letters was expected to induce a local movement-time increase due to the specific co-articulation demands associated with having to fluently connect the pre-programmed within-letter strokes by means of an ad-hoc constructed between-letter connection stroke (cf. Meulenbroek and Van Galen, 1989). The use of alternating versus repeating letter pairs was further meant to vary the letter-connection complexity according to the following rationale. At the level of individual up and down strokes, these letter pairs contained a confusingly large number of repetitions of quasi-similar pen-tip trajectories. For the realization of these writing trajectories in real time, it is assumed that they are downloaded to the muscle-initiation stage letter-by-letter and stroke-by-stroke from a Short Term Motor Buffer (Van Galen et al., 1989). At the letter level, this means that because of the higher degree of confusability of identical elements in the Motor Buffer, the repetition of either the letter *n* or *m* – in the letter pairs *nm* and *mm*, respectively – was expected to slow down the upstroke towards the second (identical) letter. Having to write the letter pairs *nn* and *mm* was therefore expected to induce a local reduction in handwriting speed due to the more difficult retrieval of the oncoming element from a similar set of elements (Van Galen et al., 1986). In addition to these local task-complexity variations, an external stressor was used to influence movement speed globally. For this purpose, participants were presented by means of headphones with a 75-dB distracting sound in half of the trials (Van Gemmert and Van Galen, 1998).

2.5. Procedure

After having read the written instructions and having agreed to participate, the subject’s arm was cleaned at the locations where the EMG electrodes were to be attached. The eight

muscles that we selected to capture the muscular activity of the participant's forearm were (1) m. extensor carpi radialis longus, (2) m. extensor carpi ulnaris, (3) m. extensor digitorum, (4) m. abductor pollicis longus, (5) m. flexor carpi ulnaris, (6) m. flexor carpi radialis, (7) m. adductor pollicis, and (8) interosseus dorsalis I. EMG electrodes were placed in a bi-polar derivation with an inter-electrode distance of 2 cm, parallel to the fibers at the bellies of the muscles under study (for electrode placements, see [Delagi and Perotto, 1994](#)). The reference electrode was placed on the epicondylus lateralis humeri. The electrode locations were prepared by cleaning and rubbing the skin with alcohol and gel, until skin resistance was below 10 k Ω . EMG activity was sampled at 2 kHz (Common Mode Rejection Ratio 90 dB, high-pass 20 Hz, low-pass 500 Hz). The EMG signals were visually inspected for quality at rest, low intensity, and maximum contraction. Especially poor electrode-skin contact can evoke large artifacts in the EMG signal. Electrode placement was checked by letting the muscles contract at their specific function with the aim to prevent cross-talk from adjacent muscles affecting the EMG recordings. If necessary, we adjusted the electrode placement, until reliable signals were obtained. Subsequently, the participant was allowed some practice trials (less than 10 per subject) to familiarize him or herself with the experimental set-up. The sequence of events that occurred in a single trial is depicted in [Fig. 2](#).

The stimuli were projected from below the table onto a translucent screen (30 cm \times 20 cm) that was built into the tabletop. By means of a single-reflective mirror positioned below, the tabletop at an angle of 45 $^\circ$, the LCD projections were clearly visible to the participant. Two seconds after the start of each trial, an ellipsoidally moving cursor was projected onto the translucent screen. The cursor movements were generated on the basis of [Hollerbach \(1981\)](#) definitions of cyclical handwriting-like movements as defined by a simple coupled-oscillator model. The frequency of the horizontal and vertical, sinusoidally-oscillating components were both set at 3 Hz, the amplitudes of these components were 2.5 and 5.0 mm, respectively, and their phase difference amounted to 70 $^\circ$. The projection system was also used to present the participant with the required letter pair in each trial, first presented in red as a precue of the upcoming handwriting task, and 2 s afterwards turning into black as a cue to start making the transition from performing the ellipsoidal drawing movements to writing the indicated letter pair. A paper strip was positioned immediately below the projection area. Participants were asked to place their non-dominant hand on this paper strip to prevent it from moving while they performed the task. The IRED-position data were sampled at a rate of 200 Hz with a spatial accuracy that was better than 0.2 mm in X, Y, and Z dimensions. In between trials, a 5-s pause was used in which the participants were asked to move the paper leftward approximately 10 cm.

2.6. Signal pre-processing

Pen-tip displacements were filtered with a low-pass, third-order Butterworth filter applied twice with a cut-off frequency of 10 Hz. [Fig. 3](#) shows an example of the filtered writing trace as obtained in a typical trial. The horizontal and vertical pen-tip position–time functions were derived and displayed for inspection (see bottom graph in [Fig. 4](#)). Next, the extrema in the vertical position–time function were identified by means of an automatic

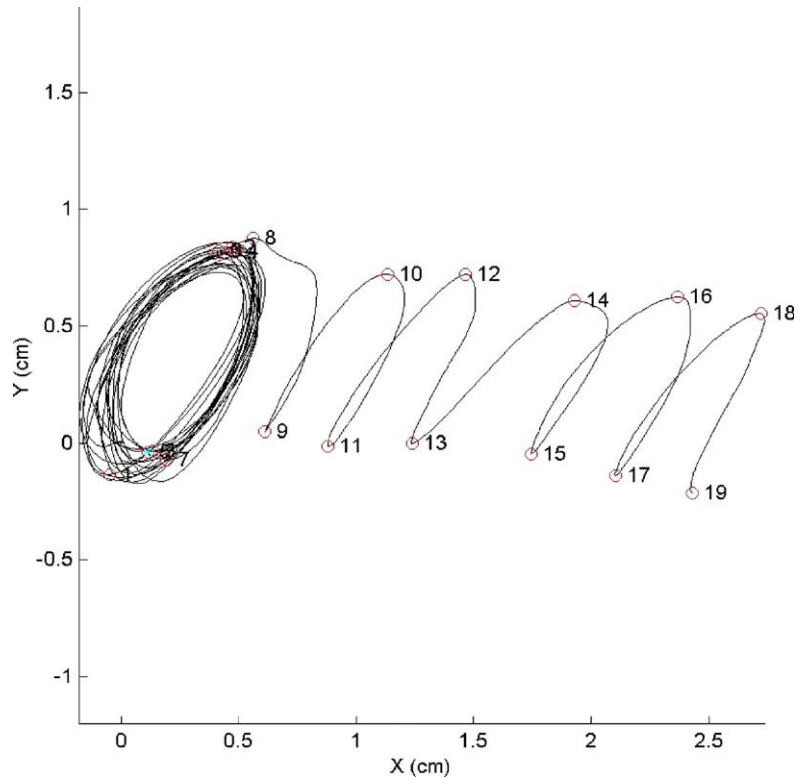


Fig. 3. Example of digitized pen-tip displacements in a trial, in which the ellipsoidal drawing movements were followed by the production of the letter combination 'mm'. Numbers indicate the locations in the writing trace at the moments of extrema in the corresponding low-pass filtered vertical pen-tip position–time function (see Fig. 4, bottom graph).

search procedure, the results of which were also visually inspected (see the circles after $t = 7$ s in Fig. 4).

Pre-processing of the raw EMG data consisted of applying a Root Mean Square filter with a time constant of $t = 0.02$ s, which resulted in a rectified, filtered surface EMG signal for each of the eight muscles. To synchronize the EMG signals with the IRED-position recordings, a constant time shift of 50 ms was applied to compensate for the plant, i.e., EMG/muscle-force, delay. Even though the plant delay may vary from muscle to muscle, we opted for using a constant time shift of 50 ms for all muscles, since this was considered a conservative procedure in a situation in which the plant delay of the individual muscles under study could not be assessed reliably. Finally, a third-order, low-pass Butterworth filter with a cut-off frequency of 10 Hz was applied twice to focus the analyses on variations in the surface EMG measurements that corresponded with the pen-tip displacements.

The EMG data were normalized with respect to their amplitude in a task-relevant fashion. In particular, the pre-processed and low-pass filtered EMG signals of each trial

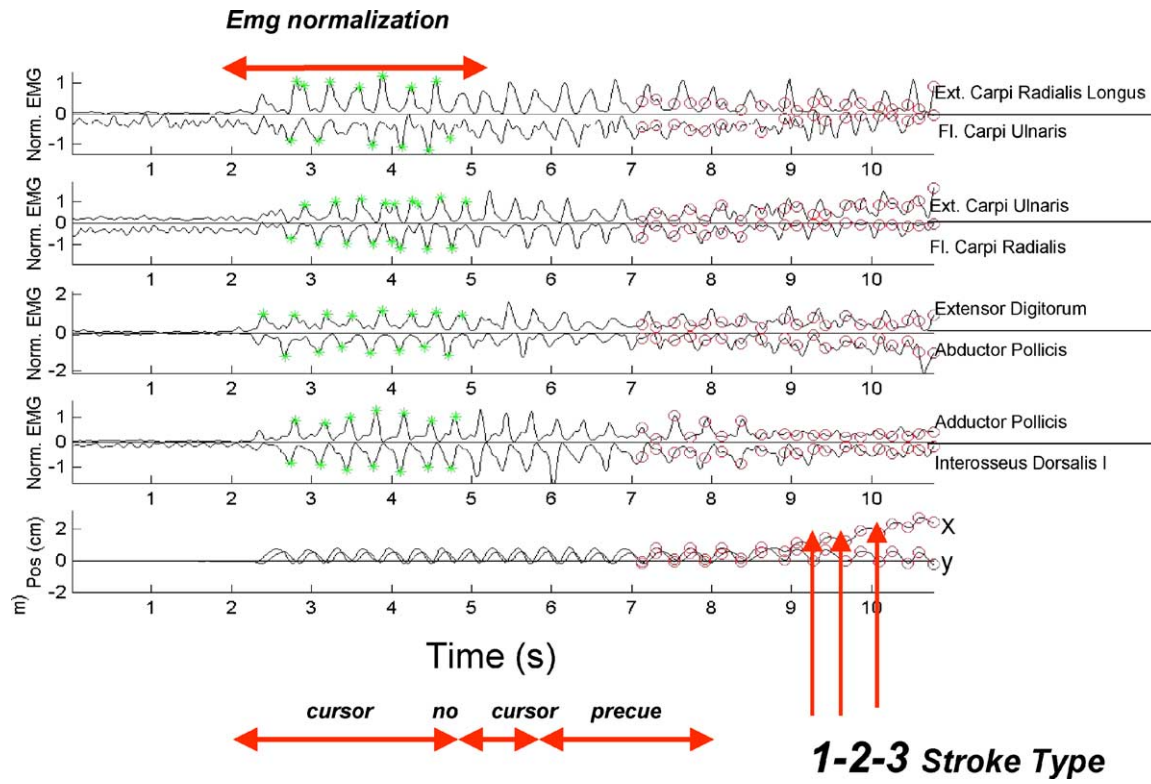


Fig. 4. Example of pre-processed and filtered EMG signals (top four graphs) and horizontal and vertical pen-tip position–time functions (bottom graph) as obtained in a typical trial. From top to bottom, the activities of the m. extensor carpi radialis longus, m. extensor carpi ulnaris, m. extensor digitorum, and m. adductor pollicis are displayed on the positive Y-axis of the upper four graphs, respectively. Similarly, the activities of the m. flexor carpi ulnaris, m. flexor carpi radialis, m. abductor pollicis, and m. interosseus dorsalis, are shown on the negative Y-axis of the upper four graphs, respectively. Peak EMG values as observed during the ellipse-drawing phase between $t = 2$ and $t = 5$ s are represented by asterisks. Extrema in the vertical pen-tip position–time function after $t = 7$ s are represented by circles.

were subjected to a peak-detection algorithm identifying the maximum EMG values that were recorded in each of the eight muscles during the externally paced ellipse-drawing phase of each trial. A peak in the EMG signal was defined as a local maximum that exceeded the mean EMG signal plus one standard deviation as measured during the externally paced ellipse-drawing phase. Having found these peak EMG values for a particular muscle (see the asterisks between $t = 2$ s and $t = 5$ s in the EMG signals displayed in the top four graphs of Fig. 4), the EMG signal of that muscle was divided by the mean of the identified peak EMG values. For each muscle and trial separately, this amplitude normalization resulted in the EMG signals being expressed in units of the average of the maximum EMG values that were attained during the externally paced ellipse-drawing phase.

2.7. *Dependent variables*

The kinematics of the pen-tip displacements during the ellipse-drawing phase of each trial were captured by calculating the mean movement time (in seconds), mean trajectory length (in centimeter), and mean peak velocity (in centimetre per second) of the upstrokes that were produced in the 3-s interval during which the moving cursor was presented, in the subsequent 1-s interval during which the moving cursor was absent, and the following 2-s interval during which the precue was presented, separately (see Fig. 2). Upstrokes were identified by determining successive extrema in the vertical (Y) position–time function in between which the pen-tip moved in the positive Y -direction. For the handwriting phase of each trial, the movement time, trajectory length, and peak velocity of three, spatially comparable, upstrokes were calculated, viz., the first upstroke of the first letter, the upstroke constituting the letter connection, and the first upstroke of the second letter (marked 1–2–3 Stroke Type in Fig. 4).

EMG levels during the three time intervals of the ellipse-drawing phase and of the three upstrokes of the handwriting phase of each trial were assessed by calculating the mean normalized EMG level for each muscle separately. Of each upstroke that was isolated in the data analysis, the corresponding vertical pen-tip velocity–time function was determined and the time windows of the accelerative and decelerative phases for that upstroke were identified. Subsequently, the EMG signal of each muscle during pen-tip acceleration was correlated with the vertical pen-tip velocity function. The resulting eight correlation coefficients that were thus found were rank ordered. The muscle of which the EMG signal correlated maximally positive with the vertical pen-tip velocity–time function was identified as the functional agonist, and the muscle of which the EMG signal correlated maximally negative with the vertical pen-tip velocity–time function was identified as the functional antagonist during that phase.² The same procedure was repeated for the decelerative part of the upstroke.

² One could argue that the acceleration–time function could have better been used to determine the functional agonists and antagonists because in general acceleration corresponds more closely to force production and thereby to EMG data than velocity. However, the correlations reflected the correspondence between the changes in velocity (i.e., acceleration) and the changes in the preprocessed surface EMG data. Moreover, a separate analysis involving the acceleration–time functions yielded a less consistent pattern of results probably due to the inherently larger variability in the second derivative of the position–time functions.

Both the muscle identity and the correlation coefficients were stored for subsequent analyses. In addition, two co-contraction indices of the thus isolated functional antagonistic muscle pair were calculated, viz., the normalized mean activity of the antagonist divided over the sum of the mean activity of the agonist and antagonist, multiplied by 100 in order to express co-contraction as a percentage. In a similar vein, i.e., also for the accelerative and decelerative parts of each produced upstroke separately, the time difference between the moments at which the agonist and antagonist peaked was investigated. This parameter yielded, however, no systematic effects and will therefore not be described further.

2.8. Statistical evaluation

The dependent variables extracted from the ellipse-drawing phase were evaluated separately from those obtained in the handwriting phase. The trials in which single letters were written were excluded from the data analyses, since these trials were not needed to test the key prediction of the present experiment and could therefore be considered filler trials. For the ellipse-drawing phase, the means of each dependent variable across the 12 replications of a task condition (6 in each of the ABBA and BAAB trial blocks) per subject were subjected to repeated measures ANOVAs according to a 10 Subjects \times 2 Noise Levels (white noise absent versus present) \times 3 Epochs (Epoch 1: moving cursor present, Epoch 2: moving cursor absent, and Epoch 3: precue present) factorial design. For the handwriting phase of the experiment, the means of each dependent variable across the 12 replications of a condition per subject were subjected to repeated measures ANOVAs according to a 10 Subjects \times 2 Noise (white noise absent versus present) \times 4 Letter Combinations (*nm*, *nm*, *mm*, and *mm*) \times 3 Stroke Type (1st within-letter upstroke 1st letter, between-letter upstroke, and 1st within-letter upstroke 2nd letter) factorial design. Repeated measures data were checked for violations of sphericity (Greenhouse-Geisser) and *F*-value that proved statistically significant after having adjusted the probabilities are reported. The correlations observed during the procedure to identify the prime movers were evaluated after applying the Fisher-*z* transformation.

3. Results

3.1. Kinematics of ellipse drawing

To verify whether the external stressor elicited the predicted global movement-time increase, the kinematics of the ellipse-drawing movements that preceded the handwriting movements were analyzed. Fig. 5 shows the mean movement time, trajectory length, and peak velocity of the upstrokes produced in the ellipse-drawing phase. The external stressor induced a small, but systematic movement-time increase ($F(1,9) = 6.86$, $P < 0.05$) that could not be attributed to trajectory-length variations ($F(1,9) < 1$, ns). Towards the end of the ellipse-drawing phase subjects gradually realized lower peak velocities ($F(2,18) = 14.04$, $P < 0.01$). No further main effects or interactions were found.

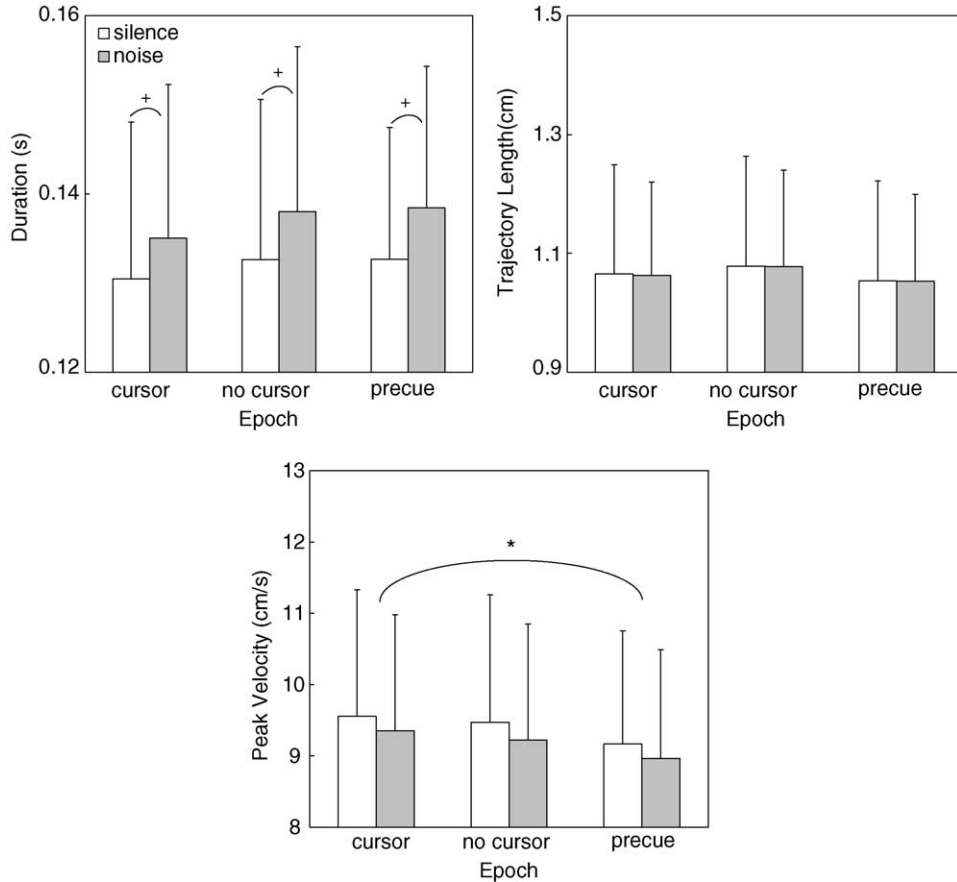


Fig. 5. Kinematic features of the upstrokes in the ellipse-drawing phase. Mean duration in seconds (left-hand panel), trajectory length in centimeter (middle panel), and peak velocity in centimeter per second (right-hand panel) as a function of Epoch (moving cursor, no cursor, precue) and External Stress Factor (silence vs. 75-db white noise). Error bars represent standard deviations; $^+P < 0.05$; $^*P < 0.01$.

3.2. Co-contraction during ellipse drawing

To verify whether the global movement-time increase due to the external stressor was accompanied by increased levels of co-contraction, the co-contraction level during the ellipse-drawing phase was analyzed. Fig. 6 shows the mean co-contraction levels expressed as a percentage of the summed activity of the prime movers in the ellipse-drawing phase for the accelerative and decelerative parts of the upstrokes, separately. During pen-tip acceleration, only marginal variations in co-contraction levels of the prime movers were found (see the top-left panel in Fig. 6). The interaction between Noise and Epoch ($F(2,18) = 5.35$, $P < 0.05$) showed, however, that in the first and last Epoch of the ellipse-drawing phase, co-contraction was higher in the condition in which the distracting sound was present, but this was not the case in the intermediate stage when the moving cursor was

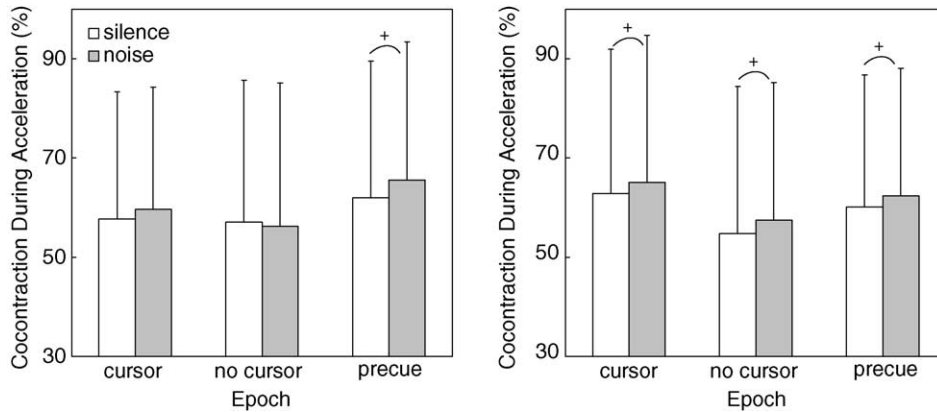


Fig. 6. Co-contraction indices as observed in the functional antagonistic muscle pairs identified in the upstrokes in the ellipse-drawing phase as a function of Epoch (moving cursor, no cursor, precue) and External Stress Factor (silence vs. 75-db white noise). Mean co-contraction levels in percentages in the accelerative phase (left-hand panel) and in the decelerative phase (right-hand panel). Error bars represent standard deviations; $^+P < 0.05$; $^*P < 0.01$.

absent. Apparently, the combination of the presence of the external sound stressor together with the visually presented task demand (either the moving cursor or the precue) provoked the higher levels of co-contraction. Neither further main effects or interactions were found nor did the experimental factors have any effect on the phase difference between the prime movers.

During pen-tip deceleration, a main effect of Noise was found ($F(1,9) = 5.24$, $P < 0.05$; see the top-right panel in Fig. 6), showing that co-contraction of the prime movers increased a few percentage when the distracting sound was present. Neither further main effects or interactions were found nor did the experimental factors have any effect on the phase difference between the prime movers.

3.3. Kinematics of handwriting movements

To verify whether the local speed reductions that were expected to occur during the writing of the letter pairs were present, the kinematics of the handwriting movements were analyzed. Fig. 7 shows the mean movement time, trajectory length, and peak velocity of the targeted upstrokes produced in the handwriting phase. The results are pooled across the Noise factor, since this manipulation did not show any effect on the handwriting kinematics. The movement time of the between-letter upstroke (left-hand panel in Fig. 7) was systematically longer than that of the within-letter upstrokes ($F(2,18) = 5.17$, $P < 0.05$). The factor Letter Combination also elicited movement-time variations ($F(3,27) = 10.92$, $P < 0.01$) that replicated earlier-found effects (Van Galen et al., 1986) but these were not further scrutinized because the movement-time fluctuations needed to assess the predicted co-variation in co-contraction levels of prime movers were clearly discernable. The interaction between the factors Letter Combination and Stroke Type ($F(6,54) = 4.06$, $P < 0.05$) confirmed that the movement-time prolongation of the letter connection was

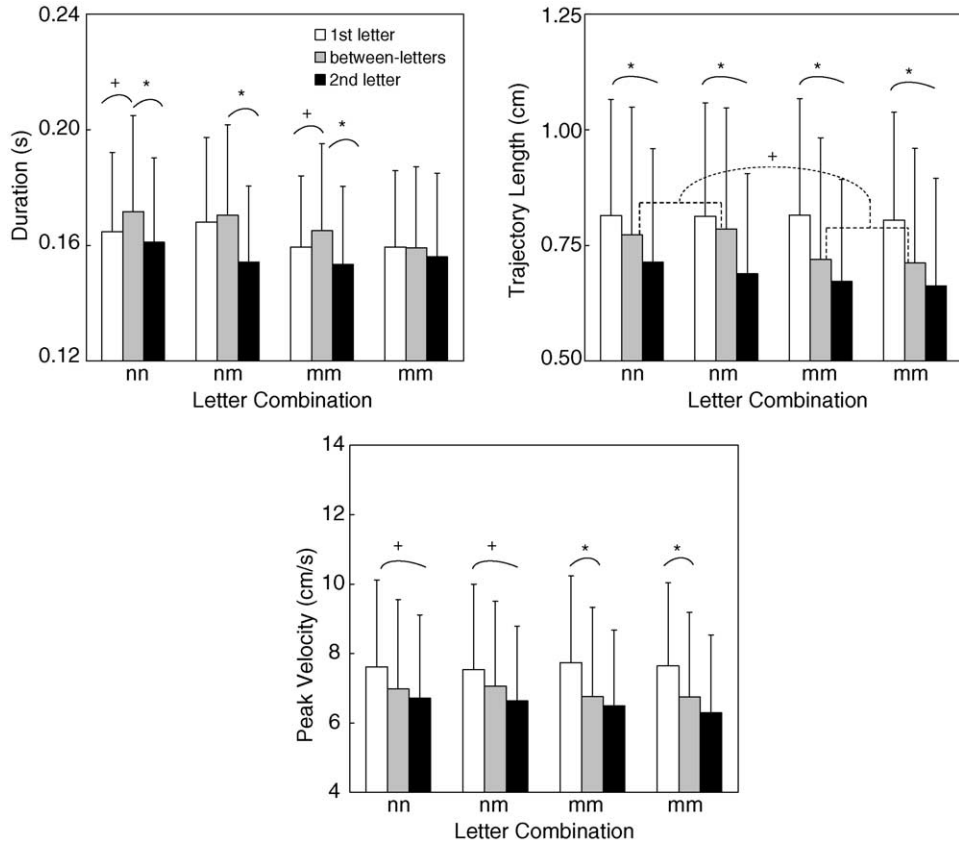


Fig. 7. Kinematic features of the upstrokes in the handwriting phase. Mean duration in seconds (left-hand panel), trajectory length in centimeter (middle panel), and peak velocity in centimeter per second (right-hand panel) as a function of Letter Combination (*nn*, *nm*, *mm*, *mn*) and Stroke Type (initial upstroke 1st letter, between letters, and initial upstroke 2nd letter). Error bars represent standard deviations; * $P < 0.05$; + $P < 0.01$.

most pronounced in the letter repetitions (*nn* and *mm*) as compared to the letter alternations (*nm* and *mn*). The just described movement-time fluctuations could not be the result of covariations in realized trajectory-length variations (middle panel in Fig. 7). As writing progressed, the trajectory length of the upstrokes systematically decreased ($F(2,18) = 24.62$, $P < 0.01$), reflecting the generally known tendency of people to reduce writing size towards the end of writing words and sentences (cf. Van Galen et al., 1986). This effect also probably induced the larger between-letter strokes in the *nm* and *nm* as compared to the *mm* and *mn* ($F(6,54) = 5.46$, $P < 0.01$), since in the latter letter pair, the connecting stroke occurred later in the stroke sequence than in the former pair. The tendency to reduce writing size towards task completion was accompanied by a reduction in peak velocities (right-hand panel in Fig. 7; $F(2,18) = 21.31$, $P < 0.01$). Again, the interaction between the factors Stroke Type and Letter Combination ($F(6,54) = 3.72$, $P < 0.05$) showed that the velocity-decrease from the 1st to the 2nd letter was larger in the *mm* and *mn* than in the *nn* and *nm*,

since in the former letter pair an additional up and down stroke needed to be produced before the letter-connection stroke was produced.

3.4. Co-contraction during handwriting

To test the key hypothesis of the present study regarding the inverse relationship between local speed reductions and increased muscular co-contraction, the co-contraction levels during the handwriting phase were analyzed. Fig. 8 shows the mean co-contraction levels expressed as a percentage of the summed activity of the prime movers in the handwriting phase for the accelerative and decelerative parts of the critical upstrokes, separately. During pen-tip acceleration, co-contraction was clearly higher in the between-letter connection strokes than in the within-letter strokes (top-left panel of Fig. 8; $F(2,18) = 10.76$, $P < 0.01$). Only a marginal trend in the predicted direction was found in the decelerative parts of the upstrokes (top-right panel of Fig. 8; $F(2,18) = 2.98$, $P < 0.10$). No further main effects or interactions were found on the co-contraction indices during the handwriting phase.

3.5. Reliability of prime-mover identification

To assess the reliability of our EMG-analysis procedure, we evaluated the statistics that were involved in the technique to identify the local prime movers. On an average, the correlations that resulted from the procedure with which, for the drawing and handwriting phase of each trial separately, we determined the functional agonists and antagonists among the eight muscles under study, were larger than 0.95. The correlations between the EMG signals and the vertical pen-tip velocity proved to be more extreme in the drawing than in the handwriting movements. This was confirmed by post-hoc paired-samples *t*-tests

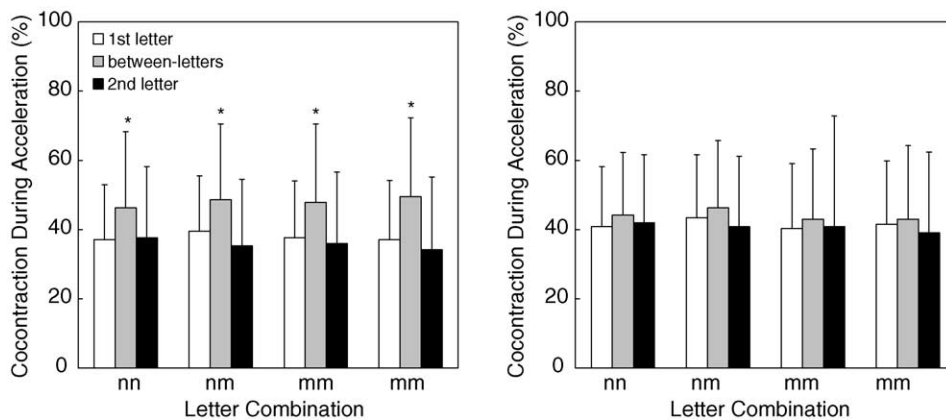


Fig. 8. Co-contraction indices as observed in the functional antagonistic muscle pairs identified in the upstrokes in the handwriting phase as a function of Letter Combination (*nn*, *nm*, *mm*, *mn*) and Stroke Type (initial upstroke 1st letter, between letters, and initial upstroke 2nd letter). Error bars represent standard deviations; * $P < 0.05$; ** $P < 0.01$.

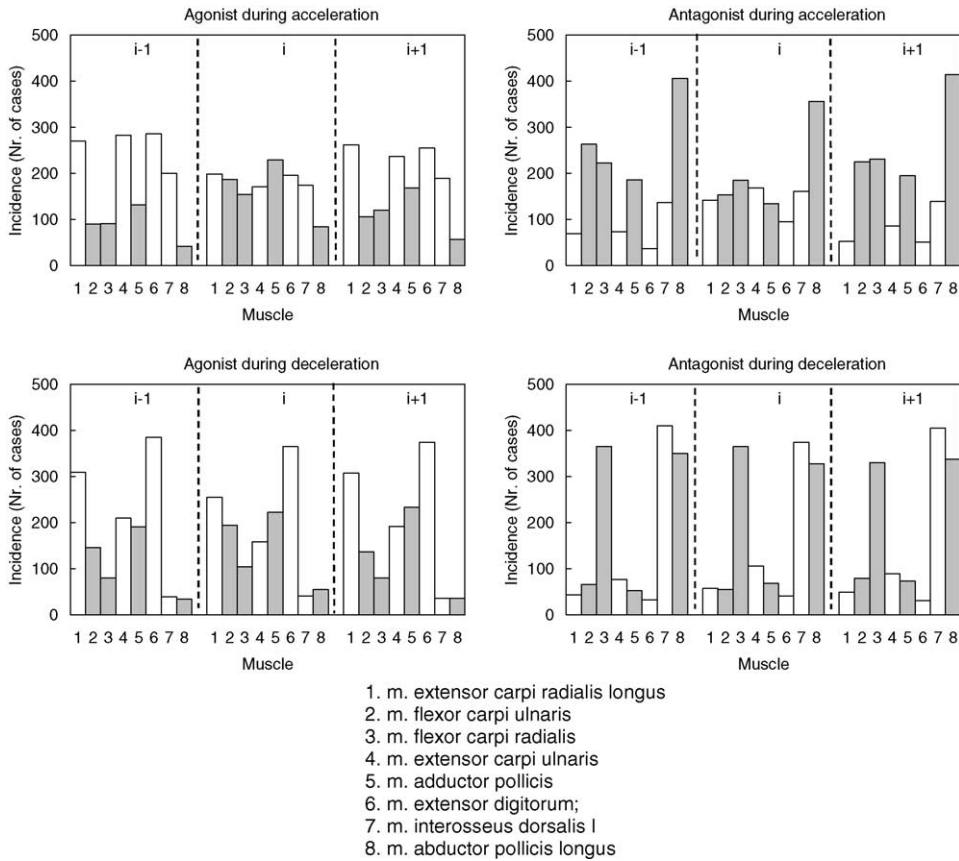


Fig. 9. Number of times each muscle was identified as functional agonist (top-left panel) or antagonist (top-right panel) during the accelerative parts of the three selected upstrokes produced in the handwriting-phase ($i - 1$: initial upstroke 1st letter, i : between letters, and $i + 1$: initial upstroke 2nd letter) of the experimental task and number of times each muscle was identified as agonist (bottom-left panel) or antagonist (bottom-right panel) during the decelerative parts of the selected upstrokes. White bars refer to extensor and grey bars indicate flexor muscles.

on the average correlations of each subject in each of the data categories shown in Fig. 9 ($t_{acc}(9) = -3.42$, $P = 0.008$, $t_{dec}(9) = -2.168$, $P = 0.058$ for the agonists and $t_{acc}(9) = 3.264$, $P = 0.010$, $t_{dec}(9) = 3.610$, $P = 0.006$ for the antagonists, respectively).

Fig. 9 displays the frequency with which each muscle was identified as functional agonist (left-hand panels) or antagonist (right-hand panels) in the accelerative (top panels) and decelerative parts (bottom panels) of the three selected upstrokes in the handwriting phase of each trial. The results are summed over participants, which obscures individual differences. The frequency distributions support the reliability of the algorithm that we designed to identify local agonists and antagonists from among the set of eight forearm muscles that we examined. In particular, the algorithm resulted in a differentiation of extensors and flexors as agonists and antagonists during the acceleration and as antagonists and agonists during the deceleration in the up strokes.

4. Discussion

In the neuromotor noise theory of goal-directed movements that was originally formulated to explain Fitts' Law (Van Galen and Schomaker, 1992; Van Galen and De Jong, 1995), Van Gemmert and Van Galen (1997) claim that increased muscular stiffness is a likely mechanism to slow down movements in complex motor tasks like drawing and writing whenever increased cognitive demands have to be coped with. According to this theory, stiffness control functions as a low-pass filtering mechanism to increase the signal-to-noise ratios of neuromotor signals when these signals happen to be impoverished by increased task demands or conditions of physical, emotional, and/or psychosocial stress (see also Van Galen and Van Huygevoort, 2000).

Whereas the external sound stressor induced a co-contraction based movement-time increase in the ellipse-drawing phase of the experimental task, the complex letter-connection production in the clockwise rotating letter pairs *nm*, *nm*, *mm*, and *mn*, induced such an effect in the handwriting phase. Both these effects could not be attributed to a covariation between trajectory length and movement time. The present findings therefore demonstrate that external stressors and cognitive and psychomotor factors may cause movement-time prolongations that are accompanied by an increase in limb stiffness (see also Van Loon et al., 2001 for similar effects due to mental-load variations). The former effect was subtle, since it was not found in the handwriting phase. The letter complexity effects apparently overruled the external-stressor effects probably because of attention primarily being drawn to the writing task.

On the basis of the assumption that limb displacement is ruled by the laws governing mass-spring systems, this would not have been expected (Latash and Zatsiorsky, 1993). On the contrary, on the basis of equilibrium-point models that emphasize the mass-spring characteristics of muscles and tendons, increased co-contraction should have been accompanied by a decrease in movement time (Bizzi and Mussa-Ivaldi, 1990; Feldman, 1986; Gomi and Kawato, 1997). In the neuromotor noise theory, however, a different view on the role of limb stiffness is proposed. Here, limbs are seen as moving rigid bodies, best described by classical Newtonian movement equations (see Footnotes 1 and 2). Stiffness in this model has two partly opposing effects. On the one hand, increased co-contraction enhances the resistance to change and, therefore, enlarges stiffness. Higher stiffness has beneficial effects on the noise-filtering characteristics of the limb displacement system as demonstrated in the simulation study by Van Galen and De Jong (1995) and as empirically shown in humans by Van Galen and Schomaker (1992). Other authors who have pointed to the beneficial effects of higher co-contraction regimes on inherently noisy motor systems are Seidler et al. (2002) and Gribble et al. (2003). On the other hand, higher stiffness causes less effective movement strategies because of the lowered gain factor.

In Section 1, we suggested that the relationship between co-contraction and the speed of movement would provide a possible answer to the question, how the speed of central information processing covaries with the pace of executorial processes at the motor level. Although in the early days of human performance theory quite often a strictly serial model of information processing was defended nowadays no one can longer defend the view that motor execution does not go in parallel with preparing oncoming tasks elements. Especially complex tasks like language production, drawing, and gesturing are typical

concurrent tasks in which higher levels of information processing concur in parallel to lower level executive processes. In a model of the production of handwriting, Van Galen (1991) proposed that the more abstract, language related processors that are involved in this task work at the more remote (i.e., more future) aspects of the task whereas lower motor execution systems realize motor output of earlier processed symbolic stages. For the fluent production of the writing it is necessary that if, because of more intensified processing at higher levels of the system (e.g. if a difficult spelling of a word has to be retrieved from the lexical spelling system), these higher layers of the system are delivering their output to the motor systems at a lower pace, there should be a provision that the ongoing motor output is slowed down to a degree that is in accordance with the processing load at the higher level. In the neuromotor noise theory, there is such a provision for slowing down ongoing motor execution. The assumption made is that the neural system is sensitive to the overall signal-to-noise ratio in the system. If before relaxation of the central networks this ratio is low, an automatic stiffness reflex is released with two beneficial effects. Firstly, the momentaneous motor signal is low-pass filtered by the increased stiffness and secondly, because of the decreased gain of the limb displacement system, ongoing movement is slowed down just to anticipate the delayed forthcoming of new executive commands from the higher busy system. The present experimental findings support such a theory. Two completely different task stressors had clearly discernable local and global effects on both movement time and co-contraction levels. In both cases, the direction of the relationship was identical; more co-contraction goes hand in hand with prolongation of movement time, and thus a lower movement pace. We think this is a first step towards a theory on the flow of motion as set against central processing-load theories. More steps are needed to confirm that the stiffness response is a key mechanism of movement-speed regulation. Especially different levels of task load have to be studied to design a better parameterized definition of the relationship between co-contraction and movement speed. With the experimental and psychophysiological methods exploited here, such an approach is at hands. An alternative approach would be used to analyze individual differences. An early representative of such an approach is to be found in the work of Goldstein (1964) who defended that more generalized muscular tension forms an expression of immobilization and defense. More recently, in our own work, we could demonstrate a more specific mechanism in high-anxious participants who reacted with higher levels of co-contraction to increased psychomotor task demands, exactly as the neuromotor noise theory would predict for more aroused and individuals (Van Galen et al., 2002).

An objection to the present study could be the procedure we used to identify the prime movers among the eight muscles we selected for the present study. The use of the Pearson product-moment correlation between the surface EMG signals and the vertical pen-tip velocity functions pre-supposes that the relationship between muscle activity and pen-tip kinematics is linear. Kinetics, however, generally do not linearly relate to kinematics (cf. Ostry and Feldman, 2003). However, given the small-amplitude handwriting movements under study, we considered our approach reasonable. Moreover, the high correlation coefficients that we observed (see Fig. 9) reassured us that the linear approach we took here is defensible. A consequence of having used linear correlations to identify the functional agonists and antagonists was, however, that our co-contraction estimates could be larger than 50%, implying that the mean normalized activity of the antagonist was larger than the

mean normalized activity of the agonist (see e.g. the top panels in Fig. 6). This may seem counterintuitive but in fact is not unrealistic when realizing that a conglomerate of muscles is generally responsible for movement in the context of neural cross-talk. Moreover, correlations are size insensitive, which means that the size of the agonist activity may have been underestimated. By definition, the summed activity of all muscles acting as functional agonists should be larger than the summed activity of all muscles acting as functional antagonists in order to provide the driving force need for motion. This aspect could not be verified in the present data set, since it also requires absolute maximum voluntary contractions expressed in terms of force as a basis of EMG normalization, which asks for a combination of conventional and the presently explored new EMG methodology.

As a result of the foregoing propositions, the noise-filtering characteristics of increased limb stiffness do not go without a price. Although, on an average, co-contraction levels only increased 5–10% of the combined activity of the prime movers in the present experiment, this result should, in our view, not be taken lightly in relation to the search for possible causes of writer's and other occupational cramps (Van Galen et al., 2002). When muscles are working continuously for 1 h at low intensity i.e., at less than 10% of their maximum, signs of fatigue show up (Fallentin et al., 1985; Sogaard et al., 1996). In general, muscle contraction temporarily reduces the blood flow through the contracting muscle parts. Even in a rest period following a 30 s low-intensity isometric contraction, blood flow is found to increase significantly, indicating that oxygen levels are restored back to normal and metabolites that have accumulated during the contraction can be removed (Kim et al., 1999). When we realize that in every-day motor tasks, muscle activity levels never exceed 20–30% of maximum voluntary contractions, a 5% increase in co-contraction relative to the local EMG levels that are observed, must be taken as an effect of considerable size. If such an increase in co-contraction is maintained over long periods of time, it may in the long run, have neurophysiological consequences that, in combination with lack of muscular rest and/or changed recruitment patterns, could be at the basis of the development of RSI. In an animal model (Owl Monkey), Byl et al. (1996, 1997) could indeed demonstrate that prolonged levels of co-contraction especially in distal muscle pairs of the hand has been responsible for the deterioration of receptive field specificity of the hand in area 3b of the cortex.

With respect to the origin of writer's and other occupational cramps, however, the present findings should be treated with caution. The results only partially support the recent views on the potential role of limb stiffness in RSI, since no systematic effects on the phase relationship between the prime movers were found in the present study. Increased co-contraction was not only expected to occur in the amplitude domain but also in the temporal domain, i.e., it was also expected to be reflected by a reduced phase difference between the prime movers. The absence of any effect of the task variables on the phase difference between the prime movers suggests that a permanent disinhibition of antagonistic activity as a possible neural mechanism underlying the development of writer's and other occupational cramps might only be valid for certain clinical subject groups (cf. Deuschl and Hallett, 1998; Marsden and Sheehy, 1990; Nakashima et al., 1989; Rothwell et al., 1983). In the healthy subjects that participated in the present study, evidence for this mechanism was not found.

The present demonstration of the covariation between movement-time fluctuations in continuous motor performance and muscular co-contraction levels may have repercussions for questions investigated in various other applied motor-control research contexts. Seidler et al. (1998, 2002), for example, recently showed that age-related changes in motor proficiency should probably be attributed to a gradually decreasing ability in the elderly to appropriately control muscle stiffness. Similarly, Levin and Dimov (1997) have demonstrated that in multi-joint arm movements performed by adults coping with spastic hemiparesis, disturbed stiffness control can be found, probably associated with the primary clinical symptom of increased resistance to passive movements. Besides offering potential explanations for these and related phenomena in motor control, the present study as such provides in our view an interesting alternative theoretical framework to re-assess the results of traditional chronometric analyses of temporal variations in continuous motor performance as a function of increased task demands and external stress.

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