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Motor commands for fast point-to-point arm movements are customized for small changes in inertial load

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ABSTRACT

For repeated point-to-point arm movements it is often assumed that motor commands are customized in a trial-to-trial manner, based on previous endpoint error. To test this assumption, we perturbed movement execution without affecting the endpoint error by using a modest manipulation of inertia. Participants made point-to-point elbow flexion and extension movements in the horizontal plane, under the instruction to move as fast as possible from one target area to another. In selected trials the moment of inertia of the lower arm was increased or decreased by 25%. First, we found that an unexpected increase or decrease of inertia did not affect the open loop controlled part of the movement path (and thus endpoint error was not affected). Second, we found that when the increased or decreased inertia was presented repeatedly, after 5–11 trials motor commands were customized: the first 100 ms of agonistic muscle activity in the smoothed and rectified electromyographic signal of agonistic muscles was higher for the high inertia compared to the low inertia. We conclude that endpoint error is not the only parameter that is used to evaluate if motor commands lead to movements as planned.

1. Introduction

In daily life, we perform our movements effectively under different task conditions (such as starting position, mass, etc.). If one knows all conditions in detail, one could generate motor commands that are perfectly suited for these conditions. In this paper the term motor commands refers to all supraspinal descending signals that affect the settings of spinal circuitry and alpha motoneuron activity. However not all relevant information on these task conditions is always available: for instance, we often do not know beforehand what the inertial load will be when we pick up an object. Therefore, motor control depends on the visco-elastic properties of the muscles (Van der Burg et al., 2005; Van Soest and Bobbert, 1993) and on feedback mechanisms to adjust muscle stimulation when the ongoing movement does not proceed as planned. At the level of spinal circuitry, short latency feedback mechanisms based on proprioceptive information affect muscle stimulation (Bizzi et al., 1992; Shapiro et al., 2002; Smeets et al., 1990); at longer latencies motor commands are adjusted based on information in various sensory modalities at the supraspinal level (Carlton, 1981; Jeannerod, 1988; Jeannerod and Prablanc, 1983; Todorov and Jordan, 2002). When the movement is repeated, relevant errors made in the previous movement are used to adjust the motor commands (Adams, 1971; Diedrichsen et al., 2005; Thoroughman and Shadmehr, 1999; van Beers, 2009). This way motor commands are customized for the specific task conditions of the movement.

When investigating fast point-to-point movements it is often argued that the planning of these movements aims at reducing the endpoint error (Fine and Thoroughman, 2007; Harris and Wolpert, 1998; Wei and Koerding, 2009; Woodworth, 1899). Recently Van Beers (2009) developed a model for fast point-to-point movements that customizes motor commands based only on the error in the endpoint. In this study it was found that model-based predictions of trial-to-trial adjustments in endpoint error were comparable to empirical data on fast point-to-point movements. The argument that endpoint error is used to customize motor commands is in line with theories that propose movements are controlled in a task-specific way leaving task irrelevant variability uncontrolled (Latash et al., 2002; Todorov and Jordan, 2002). These theories are elegant since they can explain how in repetitive movements task goals are achieved while the movements itself often shows high variability (Bernstein, 1996; Todorov and Jordan, 2002).

Contrary to these ideas, other researchers have proposed that in fast point-to-point movements the complete movement trajectories are planned and controlled (Diedrichsen et al., 2005; Guigon et al., 2007; Nakano et al., 1999). Researchers investigating hand path trajectories have found that hand paths are approximately straight and that linear velocity profiles are approximately symmetrical (Gordon et al., 1994; Hogan, 1984; Morasso, 1981).

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Additionally, symmetric angular velocity profiles were found in single joint point-to-point movements (Wiegner and Wierzbicka, 1992). It has been proposed that these symmetrical velocity profiles are the consequence of minimizing changes in torque or jerk (Flash and Hogan, 1985; Nakano et al., 1999).

We want to investigate if in point-to-point movements participants customize motor commands based only on the reduction of the endpoint error. We use a well-established experimental paradigm: manipulating moment of inertia in arm movements. It has been shown that this manipulation perturbed movement dynamics without affecting the endpoint error (Gottlieb, 1994; 1996; Jaric et al., 1999; Latash, 1994; Smeets et al., 1990). By using fast movements of short duration and by blocking vision of the arm, participants were neither given the time nor the information needed to adjust motor commands during movement execution.

We will first check if a relatively small (25%) and unexpected increase or decrease in inertia affects movement execution while leaving endpoint error unaffected. If this is confirmed, we will investigate whether a small increase or decrease in inertia affects motor commands after participants have become familiarized to this inertia: in other words, after they have moved with this inertia in the immediately preceding movements. If participants minimize endpoint errors only, one would expect that motor commands are not customized over trials after an inertia change is applied. If participants control movement trajectories and not just the endpoint, we expect them to anticipate the higher muscle torques needed to bring the higher inertia to peak angular velocity at 50% movement duration. In that case, we expect the initial activity of the agonistic muscles to be higher for a high moment of inertia compared to a low moment of inertia.

2. Method

2.1. Participants

Fourteen healthy subjects (eight male and six female) with a mean age of 32 years (range 24-52 years), without physical complaints at the arm, shoulder, or neck participated in the experiment. The data from one participant were eliminated from the analyses because he consistently failed to end his movements within 300 ms. The local ethical committee approved the study. After receiving information about the experimental procedures, all participants signed an informed consent written in accordance with the declaration of Helsinki.

2.2. Equipment

The participant was seated and fastened with safety belts in a seat that provided firm support of the trunk and scapula. The lower arm was placed in a manipulandum positioned at shoulder height, which fixated the thoracohumeral angle at approximately 45° adduction (in other words the length axis of the humerus making a 45° angle with the line connecting the shoulder joints). A stationary low-friction hinge aligned with the flexion/extension axis of the elbow only allowed elbow flexion and extension in a plane that was transversal relative to the trunk of the participant and that was parallel to the earth surface. The manipulandum fixated the wrist and metacarpal bones, leaving limited freedom for finger ab/adduction. Mean inertia of lower arm and the manipulandum together was 0.120 kg m^2 relative to the elbow joint.

Elbow angle was measured with a Spectrol 157 potentiometer (Vishay Electronic GmbH, Selb, Germany) installed in the rotational axis of the manipulandum. Angular acceleration at the elbow was measured with an ADXL321 accelerometer (Analog Devices, Inc., Norwood, Massachusetts, United States) installed as a single axis accelerometer at a 0.4 m distance from the rotation axis of the manipulandum. Electromyographic data was collected using a Porti sytem (TMS International BV, Enschede, The Netherlands). All data were collected at a sample frequency of 1000 Hz and synchronized with a pulse signal generated simultaneously with an audio signal that informed the participant to start a new movement.

2.3. EMG

Four pairs of surface electrodes were placed at a center-to-center inter-electrode distance of 2 cm on biceps brachii, brachioradialis, and triceps brachii (lateral head and long head) according to the procedure described on the website of the SENIAM project (http://www.seniam.org/). The EMG data were filtered bidirectionally with a high-pass filter (Butterworth, cut-off 5 Hz) to remove possible movement artifacts, rectified, and then filtered bidirectionally with a low-pass filter (Butterworth, cut-off 50 Hz). The resulting smoothed and rectified EMG (srEMG) was normalized with respect to the maximum average srEMG over a 0.5-s interval measured during maximal isometric voluntary contraction. To reduce the number of variables the normalized srEMG signals of biceps and brachioradialis were averaged (srEMG flexors), and so were the normalized srEMG signals of triceps caput longum and caput lateralis (srEMG extensors).

2.4. Experimental design

Participants performed fast elbow flexions and extensions from one target area to another. Targets were presented visually at elbow angles of 50° and 85° (with 0° indicating full elbow extension) and had a target width of 4°. A wooden board blocked vision of the moving arm, but participants were given knowledge of results once they had reached a target area by means of a laser shining from the pointing finger to the target. The laser was only visible when participants were pointing in the direction of the target. This knowledge of results was given to prevent drift in the visuomotor calibration (Smeets et al., 2006).

By adding mass to the manipulandum (out of the participant's view), three inertia conditions were created: one in which the subject moved only the lower arm and the manipulandum (0.120 kg m^2; low, L), one in which the inertia had been increased to 0.165 kg m^2 (middle, M) and one in which it had been increased to 0.205 kg m^2 (high, H). These changes correspond roughly to a 25% increase or decrease of the moment of inertia relative to the M condition.

2.5. Experimental procedure

The main measurement was performed in three blocks for elbow flexion and three blocks for elbow extension. For each movement direction two short blocks of six trials were given with either L inertia or H inertia and one long block of 60 trials was given. In 80% of these 60 trials M inertia was used, in 10% L inertia, and in 10% H inertia. In 20% of these 60 trials participants were given the impression M inertia was changed when actually it was not.

The order of movement directions (flexion before or after extension) was counterbalanced over participants. Within each movement direction the three blocks were offered in randomized order. Before starting a new block participants were allowed five trials to familiarize themselves with the movement and the inertia. Before the start of each trial participants were asked to point at the first target and wait for the auditory starting signal, then look at the second target and make a movement from the first to the second target area as fast as possible. All inertia changes were applied just before the starting signal. To prevent exploration of the load participants were not allowed to move the manipulandum before the start of a new trial.

2.6. Data processing and statistics

Both elbow flexions and extensions were performed in three blocks. Only trials that had a certain history were analysed. For the long block in which the participants were familiarized with M inertia, the L trials (ML) and H trials (MH) always followed after 3-5 M trials, and were all analysed. All M trials following the L trials or H trials were discarded. The remaining M trials were analysed (MM). In the remaining two blocks participants were familiarized with L or H inertia: we analysed the L trials following five or more L trials (LL) and the H trials following five or more H trials (HH). In the ML, MM and MH conditions the L, M and H inertia was supposedly moved under identical motor commands since participants had no way of knowing the inertia and no time to adjust during the movement. These conditions were used to establish how the small inertia changes affect movement kinematics. The LL and HH conditions were used to investigate if motor commands are customized for small inertia changes. We realize that after eleven trials participants may not have fully customized their motor commands. Yet 11 trials are sufficient to see if motor commands are customized for the inertia while endpoint error remained unaffected which is the aim of our research.

Movement onset was defined as the first sample after the auditory cue was given in which angular acceleration exceeded 15% of the peak acceleration. For each participant we determined the elbow angles corresponding to pointing at the targets by averaging over all trials in the same movement direction, the elbow angle just before movement onset. This elbow angle was calculated by taking the mean angle over a time period of 50 ms after the auditory starting signal was given. This target-elbow angle calibration was used to determine the initial overshoot of the movement. To see how inertia changes affect endpoint error and movement trajectories, several kinematic parameters were calculated. The reversal point of the movement was defined as the instant after movement onset at which absolute angular velocity dropped below 5°/s. Oscillations or corrections (referred to as submovements) occurred in most trials after this reversal point. For our present purpose, it is more important that at this point in time the movement is still fully determined by open loop motor commands and feedback mechanisms on spinal and muscular level. If movement amplitude would fall short in the MH condition compared to the MM or ML condition due to the additional inertia we expected this to show at the reversal point as previously defined. We took the difference between the angle at the reversal point and the angle when participants pointed at the target area (overshoot or *OS*) as a measure of how the open loop controlled part of the movement path is affected by inertia changes. If inertia changes have no effect on the open loop controlled movement path it is not likely that participants change their motor commands in order to reduce endpoint error.

We also determined whether inertia changes affected the number of submovements after the reversal point, since some researchers propose that the energy cost of these submovements are taken into account in movement planning (Elliott et al., 2004; Lyons et al., 2006; Oliveira et al., 2005). Note that in this phase of the movement participants received feedback on their movement, allowing motor commands to be adjusted based on supraspinal feedback mechanisms. We determined the submovements by tracing the subsequent instances after movement onset at which absolute angular velocity dropped below 5°/s. We defined n_{sub} as the number of submovements from the reversal point to the point where the amplitude of the submovements dropped below 2°.

Additionally, peak angular velocity (ω_{peak}) and time to peak angular velocity relative to the total movement time (t_{acc}) were calculated. A t_{acc} of 0.5 means that velocity profiles are symmetrical: duration of the acceleration phase is equal to duration of the deceleration phase. To quantify how movement kinematics changed with inertia the dependent variables *OS*, n_{sub}, ω_{peak}, and t_{acc} were compared between the ML, MM and MH conditions with repeated measures ANOVAs and post hoc *t*-tests, using Bonferroni corrections.

To see how inertia changes affected motor commands, the first 100 ms of the measured electromyographic activity (EMG) of the elbow flexors and extensors were compared between the LL and HH conditions. This part of the EMG is considered to originate from open loop motor commands since it has been shown to be unaffected by unexpected blocking or perturbing the movement (Shapiro et al., 2004; Smeets et al., 1990; Wadman et al., 1979). For every participant the normalized srEMG data for all trials within one condition were aligned based on movement onset and averaged to one curve for elbow flexors and one curve for elbow extensors.

Aligning the srEMG signals based on movement onset might introduce a confounder; movements performed in the low inertia condition might reach the acceleration threshold for detection of movement onset earlier after the start of the first agonistic muscle activity than movements performed in the high inertia condition. We anticipated this by using an acceleration threshold relative to the peak acceleration; indeed, compared to a fixed threshold, movement onset was detected on average 2.5 ms later for L loads and 2.5 ms earlier for H loads. We confirmed that alignment of srEMG signals based on movement onset resulted in properly aligned EMG traces. This was achieved by calculating the time shifts of HH relative to LL that resulted in optimal alignment. Only for 5 out of the 26 cases (13 for elbow flexions and 13 for elbow extensions), a small shift varying between −7 ms and +3 ms improved alignment. So our method does not introduce artefacts.

The srEMG curves for agonistic muscles were compared between HH and LL conditions by time-integrating the difference signal HH–LL from −50 till 25 ms relative to movement onset (we will refer to this as "early srEMG"). This time interval is well within the range of the first 100 ms of the agonistic muscle activity for which literature (Shapiro et al., 2004; Smeets et al., 1990; Wadman et al., 1979) suggests that muscle activity is determined by open loop motor commands. This resulted in one number per participant, which is positive if agonistic srEMG was higher in the HH than the LL condition (see Fig. 3, grey area's). Since we hypothesized that we would find a positive time-integral between the HH and LL signal we used a one-tailed paired-sample *t*-test ($\alpha = 0.05$) to test whether the predicted effect was present in the data.

3. Results

As an example, we show the kinematic and electromyographic data for the flexion trials recorded in participant 12 (Fig. 1). Fig. 1A shows the mean data measured when moving with an L or H inertia conditions after the participant had familiarized himself with M inertia (ML or MH). These conditions were used to see how movement kinematics were affected by the modest change in inertia. Fig. 1B shows the mean data measured under L or H inertia after participants had been familiarized with this inertia (LL or HH). These conditions were used to see if agonistic early srEMG (grey areas in Figs. 3 and 4) was affected by the modest change in inertia.

3.1. How do small inertia changes affect movement kinematics?

To answer this question, we study the difference between the various conditions in which the subjects were familiarized with the M inertia. Fig. 2A (black symbols) shows that *OS* did not differ

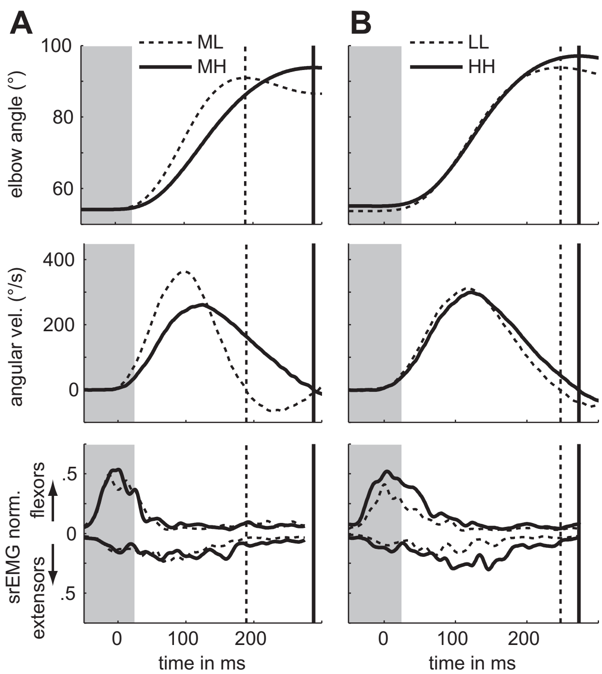

Fig. 1. Example of kinematic data and normalized srEMG for the elbow flexors, summed over biceps and brachioradialis, and normalized srEMG for the elbow extensors, summed over triceps caput longum and caput laterale. Data are averaged over the six trials within each condition. (A) L inertia or H inertia was given after participant had familiarized himself with M inertia. (B) L inertia or H inertia was given after participant had familiarized himself with this inertia. Grey areas indicate the time periods of the early srEMG, which is assumed to be based on open loop motor commands. Vertical lines indicated the reversal point of the movement. Mean data of participant 12 are shown.

between the ML, MM and MH conditions (test results and *p*-values are given in Table 1). This means that for a 25% decrease or increase in inertia the motor system was still successful in reaching the target. The fact that *OS* was positive means that irrespective of the condition, subject's first stop was beyond the target area.

A closer look at the data (see Fig. 2A and Table 1) revealed a significant increase in the number of submovements n_{sub} for the ML condition and a decrease for the MH condition. This means that the movement after the reversal point was affected by the inertia changes. Not surprisingly, peak angular velocity ω_{peak} was affected by inertia changes: ω_{peak} was higher for the ML condition and lower for the MH condition. Also the relative time to peak velocity t_{acc} was affected by inertia changes: t_{acc} was higher for the ML condition and lower for the MH condition. This means that the inertia changes affected the symmetry of the velocity profiles.

3.2. How does familiarization with modest inertia changes affect motor commands?

Fig. 3 shows the agonistic srEMG measured during elbow flexions for the LL and HH conditions for all thirteen participants. A clear pattern is present in the early srEMG time window (grey area Figs. 3 and 4A): agonistic srEMG is significantly ($t_{12} = 3.24$, $p = 0.004$) higher in the HH condition than in the LL condition. A similar difference was found in the extension data ($t_{12}=1.95$, $p = 0.037$) shown in Fig. 4B. This means that when participants are given the opportunity to familiarize themselves with the changed inertia the initial neural input to the muscles is changed. Considering that the initial srEMG cannot contain reflex contributions, this implies that motor commands were customized to the expected inertia.

3.3. How does customization of motor commands affect movement kinematics?

To answer this question, we compare how familiarization with modest inertia changes influences movements executed under the same inertia. In Fig. 2A (grey symbols) the kinematic parameters are shown for the LL and HH conditions, the ones in which participants were familiarized with the L or H inertia. Since we found that motor commands were customized for the LL or HH conditions, comparing kinematic parameters of these conditions with the ML and MH conditions where L or H inertia was given unexpectedly, informs on the behavioural consequences of customizing the motor commands. In Fig. 2B the mean difference between the LL and ML and the HH and MH conditions and the 95% confidence interval are shown for all kinematic parameters. The parameters that showed a relevant difference between the ML and LL, and the MH and HH conditions can be identified in this figure as the 95% confidence interval of the mean difference not including zero. One would expect parameters relevant to the motor control system to change towards more favorable values in the conditions in which motor commands are customized (LL and HH) compared to the conditions in which motor commands are not customized (ML and MH). None of the kinematic parameters used shows such changes for all four experimental conditions: elbow flexions under low and high inertia and elbow extensions under low and high inertia.

The *OS* showed an increase for all four experimental conditions (Fig. 2B), indicating that the overshoot was larger when motor commands were customized. An additional repeated measures 2 (customized/uncustomized) $\times$ 2(flexion/extension) $\times$ 2(L/H inertia) ANOVA showed a main effect on customization ($F_{1,12} = 15.81$, $p = 0.002$) indicating this increase to be statistically significant. This subscribes our finding that motor commands are customized in the LL and HH conditions. Fig. 2B also shows that for high inertia conditions the ω_{peak} values and the t_{acc} values (kinematic parameters that are affected by the inertia changes) are restored towards values found in the baseline condition (MM) when motor commands are customized. The low inertia condition did not show such restorations.

4. Discussion and conclusions

First, we established that under relatively small inertia changes one set of motor commands can successfully bring the lower arm to the target area yet with changed movement kinematics: at lower inertia, the relative duration of the acceleration phase is shorter, movement speed is higher and the number of submovements is higher. Second, our data show that after participants have become familiarized with a small inertia change, motor commands are customized to this inertia. We conclude that the adjustments of motor commands are not just aimed at minimizing endpoint error but involve more aspects of how movement is executed (e.g. movement trajectories, number of submovements).

4.1. Limitations

We found that despite the fact that we repeatedly urged each participant to move as fast as possible, not all participants were able to finish the task within 250 ms and only a few participants could do so for the condition in which high inertia was imposed. This means that in the condition in which a high inertia was given after a medium inertia most participants probably had sufficient time to adjust their motor commands during the movement based on supraspinal feedback loops. Yet during the movement only proprioceptive information on position was available. It is unlikely

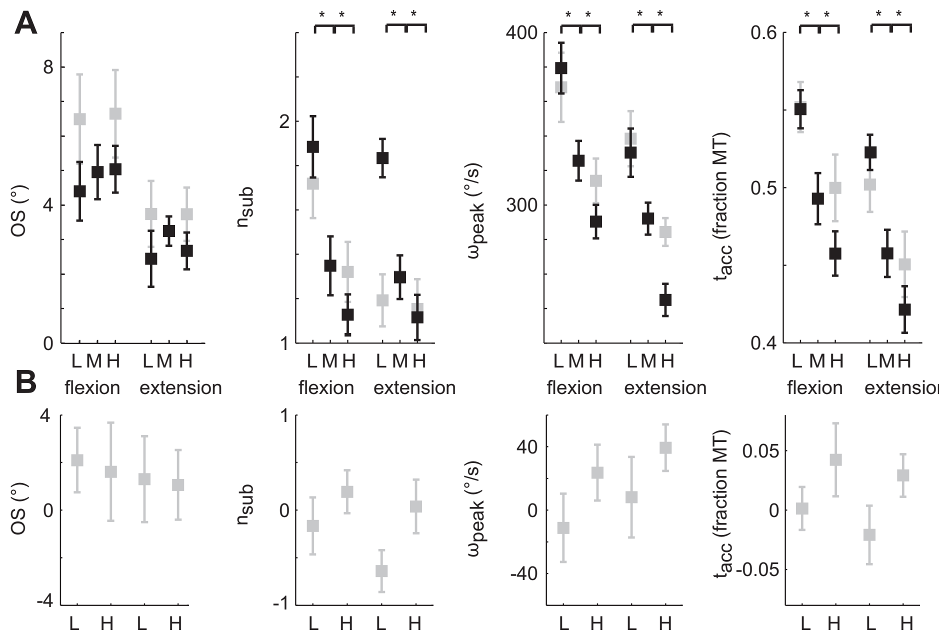

Fig. 2. Parameters describing movement kinematics are shown. (A) Black symbols indicate the conditions in which participants were familiarized with a middle (M) inertia and were given a low (L), middle (M) or high (H) inertia (ML, MM and MH conditions). Grey symbols indicate the conditions in which a low (L) or high (H) inertia was given after familiarization with the same load. Mean values over all 13 participants (squares) and the standard error of the mean (error bars) are shown. Significant differences between the ML and MM conditions and between the MH and MM conditions are marked with ∗. (B) Mean difference in kinematics and the 95% confidential interval (error bars) between the conditions in which participants were familiarized with the L or H inertia (LL and HH) compared to when they were familiarized with the M inertia (ML and MH).

Table 1
Results of the repeated measures ANOVAs (*r*ANOVAs) on the data of the block of trials in which the middle inertia was expected. First line indicates the dependent variables. The third and fourth line show the significant difference expressed as a percentage of the values found in MM condition (with standard deviation between brackets). The ML, MM and MH conditions were compared. Post hoc tests comparing ML and MH with MM were done by means of a paired *t*-test. The value for α was set at 0.025 (Bonferroni correction).

	OS		n_{sub}		ω_{peak}		t_{acc}	
	Flexion	Extension	Flexion	Extension	Flexion	Extension	Flexion	Extension
(ML–MM)/MM∗100%	–	–	52(56)	48(37)	16(6)	13(8)	12(6)	15(8)
(MH–MM)/MM∗100%	–	–	−14(16)	−13(20)	−11(4)	−16(4)	−7(4)	−8(5)
*r*ANOVA								
$F_{2,24}$	0.779	0.633	17.918	26.055	106.200	106.590	99.031	86.623
p	0.470	0.539	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Post hoc								
ML–MM								
t_{12}	–	–	3.340	5.844	9.007	5.613	8.416	8.219
p	–	–	0.012	<0.001	0.001	<0.001	<0.001	<0.001
MH–MM								
t_{12}	–	–	−3.070	−2.566	−8.900	−16.816	−6.000	−5.843
p	–	–	0.020	0.025	<0.001	<0.001	<0.001	<0.001

that this information was used to adjust motor commands because we designed the task in such a way that information on initial posture, target location and task performance was all provided visually. Therefore, vision was the only reliable information source on which to base motor commands (Pipereit et al., 2006; Sober and Sabes, 2005). Since visual information about the arm was not available until the arm reached the target area we assume that motor commands were not adjusted before the reversal point in the movement.

4.2. Did a modest change in inertia affect endpoint error?

We found that when moving under equivalent motor commands, the inertia changes did not affect the endpoint error. Yet, the number of submovements was affected in a way that seems to show a trade-off with movement speed: lower inertia leads to higher movement speed and more submovements before coming to a standstill, whereas higher inertia leads to the opposite.

We found evidence in our data that participants did not always move as fast as they could in all conditions. Early srEMG of the agonistic muscles was higher in the condition in which participants were familiarized with a high inertia (HH) than the condition in which participants were familiarized with a low inertia (LL). If the early srEMG in the HH condition can be set at a higher level one would expect that the srEMG in the LL condition might have been set higher as well, which would have led to a higher movement speed in this condition. If we assume that participants had to make a trade-off in our experimental task between moving as

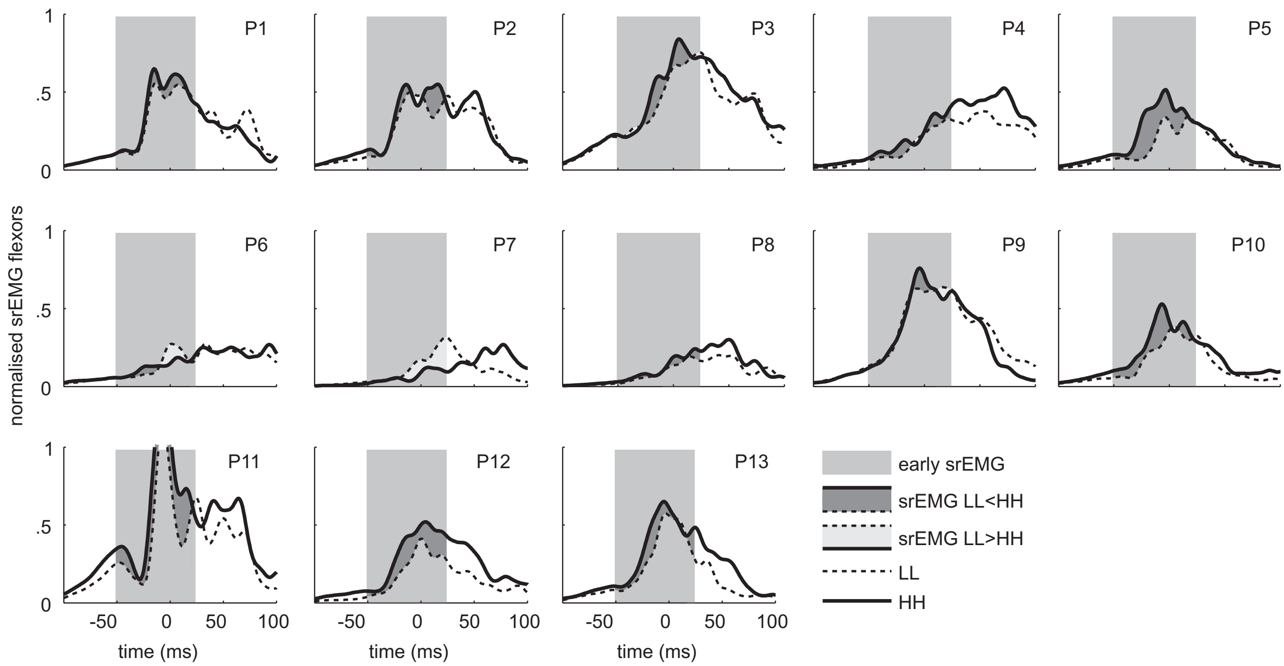

Fig. 3. The normalized and averaged srEMG signals of elbow flexor muscles plotted for each participant for the elbow flexions made under the high and low inertia after participants had familiarized with this inertia (HH and LL). The early srEMG (grey blocks) was higher for the movement made in the HH condition than for the movements made in the LL condition.

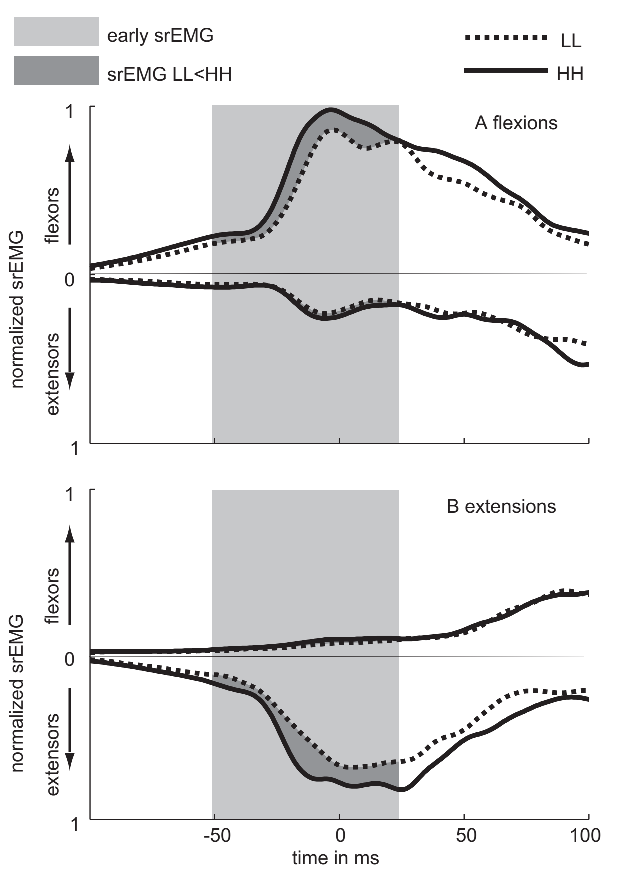

Fig. 4. Normalized srEMG of elbow flexors and extensors averaged over the thirteen participants, plotted for movements made under expected high (HH) and low (LL) inertia for elbow flexion (A) and elbow extension (B). Normalized early srEMG for the movement in the HH condition was higher than that for the movements made in the LL condition.

fast as possible and stopping the movement in a minimal number of submovements within the target area, we can conclude that the inertia changes had an effect on this trade-off (between −11% and 23%, see Table 1). This means that motor commands need to be customized for the specific inertia in order to rebalance this trade-off.

4.3. Are motor commands optimized to reduce endpoint error?

Early agonistic srEMG showed an increase for the condition in which participants were familiarized with a high inertia (HH) compared to the condition in which they were familiarized with a low inertia (LL). Our participants customize their motor commands to small inertia changes even when the endpoint error is not affected by these inertia changes. Furthermore, we found that after familiarization to the new inertia over maximally 11 trials the overshoot increased (Fig. 2B). We acknowledge that after 11 trials motor commands might not yet be optimal and that when given enough trials the motor control system might have further customized motor commands and reduce overshoot back to previous values. Yet within the first 5–11 trials motor commands were customized. This is inconsistent with previous published ideas that the humans customize motor commands purely based on endpoint error (van Beers, 2009). We conclude that humans control point-to-point movements based on other kinematical parameters than just endpoint error.

For the high inertia, it can be argued that participants adjust their motor commands (as reflected in early srEMG) in an attempt to restore the loss of peak angular velocity to values found in the baseline condition (MM). For the low inertia, a similar argument cannot be made. We have two explanations for the fact that none of the kinematic parameters showed a consistent pattern over all experimental conditions. First, our participants may have used several criteria to evaluate if motor commands lead to movements as planned. For instance trying to keep movement speed maximal, while trying to keep movement effort in homing-in phase minimal by minimizing the number of submovements. Second, complete customization to the changed inertia may not have occurred after eleven trials. Data presented in previously published research on learning to move with new movement dynamics indeed indicates that motor commands still continue to adjust after 11 trials (Cothros et al., 2006; Papaxanthis et al., 2005; Thoroughman and Shadmehr, 1999).

For future research on control of point-to-point arm movements we suggest to further investigate what criteria humans use to customize motor commands by using experimental paradigms that change movement kinematics without affecting the endpoint error.

Conflict of interest statement

The authors declare that they have no conflict of interest.

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