

Vassilia Hatzitaki · Patricia McKinley

Effect of single-limb inertial loading on bilateral reaching: Interlimb interactions

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Abstract This study employed the paradigm of asymmetric limb loading during bilateral arm reaching to examine the motor system's ability to independently organize the discrete movement of both upper limbs to equidistant targets when one of the limbs is loaded under specific timing constraints. The loading procedure involved attaching two different Velcro strapped weights to the right wrist, thus increasing the right arm's mass by 25% (1 kg) and 50% (2 kg). Movements were captured by a high-speed digital camera (240 Hz), while electromyographic (EMG) activity of selected elbow and shoulder muscles of both limbs was recorded (1,000 Hz) simultaneously. The results revealed that the mechanisms used by the system to compensate for unilateral limb loading were as follows: First, addition of an inertial load resulted in an increased movement time and concomitant decrease in peak velocity of both the upper arm and forearm of *only the loaded limb* and was scaled to the added weight. Second, for the EMG parameters, adjustments to the inertial load were primarily characterized by an increase in burst duration of all muscles, with load-specific changes in activity and onset time: the elbow antagonist (biceps) demonstrated a decrease in activity with the 50% load, and the elbow agonist (triceps) had an earlier onset with the 25% load. Concomitant adjustments on the unloaded limb consisted primarily of an

increase in burst duration of the shoulder and elbow agonists (pectoralis and triceps), an earlier triceps onset solely with the 25% load, and a decrease in activity of the biceps solely with the 50% load. Third, with the exception of biceps activity, the amplitude of EMG activity was invariant across changes in load for both the loaded and unloaded limb. This lack of modulation in activity may have been related to the inability of performers to meet the time constraint of simultaneous bilateral limb arrival to the end targets. This inability can be the result of an active strategy selection process to safeguard the actions against interference or alternatively it could simply be a consequence of the biomechanical properties of the system in relation to task constraints. These issues are discussed in the light of the present findings and those of previous studies.

Keywords Bilateral reaching · Inertial load · Asymmetry · Kinematics · Electromyography · Human

Introduction

Independent load compensation by two homologous limbs when moving simultaneously is often a requirement for the skillful performance of many activities of daily living, such as when carrying different weights or moving against different loads. Several studies have explained how the motor system plans or accommodates for different inertial loads by modulating characteristics of muscle activation that will satisfy the kinematic goal of the movement to be produced (Cooke and Brown 1994; Gottlieb 1996; Gottlieb et al. 1989; Pfann et al. 1998). Gottlieb (1996) has proposed a three-element model explaining how the motor system compensates for external loads. According to this model, for fast movements performed under expected load conditions, height and width of the excitation pulses delivered to the muscles are specified by a central command, " α ," which is driven in a feed-forward manner based on an internal model of the task dynamics. However, if the central pro-

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V. Hatzitaki (✉)
Department of Physical Education and Sports Sciences,
Aristotle University, 540 06 Thessaloniki, Greece
e-mail: vasol@phed.auth.gr
Tel.: +3031-205330/992195, Fax: +3031-992180

P. McKinley
Department of Physical and Occupational Therapy, Faculty of
Medicine McGill University, Montreal, Canada, H3G 1Y5

gram fails to produce the desired trajectory and the movements are slow enough, errors in α are compensated by the “ λ ” element, which is the kinematic reference plan to which sensory feedback signals are compared and from which reflex reactions are produced. Experimental data confirm that when performers are required to keep movement time constant, increased inertial load requirements during performance of elbow flexion movements are met by increased triceps and biceps electromyographic (EMG) amplitudes, with no obvious changes in the timing of various EMG bursts (Lestienne 1979; Gottlieb et al. 1989; Sherwood et al. 1988). This adaptation has been described as a change in pulse height and has been classified as a speed-sensitive strategy (Corcos et al. 1989; Gottlieb et al. 1996). By contrast, when movement time or speed is not experimentally controlled, movements of different hand-held loads are accomplished by prolonging burst duration and increasing the area of the agonist EMG burst (Cooke and Brown 1994; Gottlieb 1996; Gottlieb et al. 1989; Lan 1997). This change has been characterized as pulse width modulation and classified as a speed-insensitive strategy (Gottlieb et al. 1989).

However, the question of how the system accomplishes its kinematic goals when load compensations for two limbs differ has not been well explored. In particular, the degree to which the loaded limb entrains the unloaded limb is a point of interest to researchers in motor control. The consideration of possible entrainment is not trivial, as it has been shown that, when the two limbs oscillate rhythmically in different coordination modes, a natural tendency toward interlimb synchronization arises; this tendency has been attributed to strong entrainment influences between the limbs (Bingham et al. 1991; Kelso et al. 1979). This entrainment is reported to be resistant to mechanical perturbations (Scholz and Kelso 1990), changes in stiffness (Bingham et al. 1991), or loading of one of the limbs (Kelso et al. 1983). On the other hand, when the interlimb coordination pattern involves the oscillation of nonhomologous limbs (i.e., hand and foot), this entrainment is reduced (Baldissera et al. 1991, 2000; Jeka and Kelso 1995). While some authors attribute this finding strictly to the difference in inertial properties or mechanical characteristics of the involved effectors (Baldissera et al. 2000), others have shown that the coupling strength between homologous limbs is greater than that between nonhomologous limbs (Serrien and Swinnen 1998), even when limbs are loaded in a way that renders inertial properties of homologous limbs more dissimilar and the nonhomologous limbs more similar. These latter investigators argue that their results are more supportive of the notion that the neural networks underlying the control of homologous limbs are more tightly coupled than those of nonhomologous limbs.

Thus, the source of this entrainment to keep the limbs synchronized is one issue that has been actively debated; whether compensation is centrally organized or is driven by peripheral mechanisms such as motion-dependent feedback is still a matter of conjecture. Originally, the

tendency of the limbs to remain synchronized during rhythmical task performance was attributed to supraspinal control centers and the influence of bilaterally distributed motor pathways transmitting commands to the periphery (Garry and Franks 2000; Kuypers 1964, 1981; Shinoda et al. 1994; Swinnen et al. 1994). On the other hand, it is suggested from recent experimental evidence that the imposed temporal synchrony in rhythmical movements is peripheral in nature and can be attributed to motion-dependent feedback that has an entraining influence upon the excitability of spinal pathways (Baldissera et al. 1991; Peper and Carson 1999; Serrien and Swinnen 1998; Swinnen et al. 1995). More specifically, it has been suggested that the central nervous system compensates for asymmetric load perturbations in order to maintain interlimb synchronization at the kinematic level by exploiting the incoming sensory information from the moving limbs (Baldissera et al. 1991; Serrien and Swinnen 1998).

The above studies provide some insight into the controlling mechanisms underlying interlimb organization under conditions in which one of the limbs is loaded or perturbed. However, the use of rhythmical or oscillatory types of task to study the complex interlimb interactions experienced with asymmetric loading may not be appropriate to explain the mechanisms underlying the organization of point-to-point or discrete movement tasks, mainly because of differences in the mechanical-inertial characteristics (Baldissera et al. 2000; Jeka and Kelso 1995) or in the innervation patterns (Pfann et al. 1998) of the involved effectors. In addition, it can be speculated that the extent of afferent influences on these interactions is also dependent on the type of bilateral movements performed. Neurophysiological adaptations of the spinal circuitry under loading can be quite different depending on whether the two limbs are moving rhythmically in different coordination modes or perform discrete tasks (Peper and Carson 1999).

A secondary issue that warrants some attention concerns the differential effect of loading on movement kinematics and muscle activation characteristics during unilateral or bilateral task performance. Natural, unrestricted reaching movements are described by straight-line hand paths and tangential velocity profiles that remain invariant across different hand-held loads (Atkinson and Hollerbach 1985; Hogan 1984; Soechting and Lacquaniti 1988). Despite this kinematic invariance, several investigators have described how muscle activation patterns change in response to added loads during movement (Gottlieb 1996; Pfann et al. 1998). The differential effect of loading on movement kinematics and muscle activation characteristics is attributed to joint-compliant properties revealed by the length-tension and force-velocity properties of the muscles that minimize the effects of external load changes on the kinematic trajectory (Gottlieb 1993). Similar effects underlie bilateral task performance. Unilateral loading (Kelso et al. 1983) or voluntary application of isometric torque by one hand during bilateral performance of isofrequency or multifre-

quency rhythms (Peper and Carson 1999) may only have a trivial influence on the temporal stability of interlimb coordination. Yet, significant interactions between the limbs are noted when the activation profiles of individual EMG bursts are examined (Baldissera et al. 1991; Peper and Carson 1999; Serrien and Swinnen 1998). Neural crosstalk or overflow between limbs, in the form of superfluous EMG activity or excess in the amount of work generated by the limb performing the simpler of the two movements, has also been observed in discrete tasks involving the simultaneous production of a unidirectional (elbow flexion) and a bidirectional (elbow flexion-extension-flexion) movement by the upper limbs (Swinnen et al. 1988, 1992).

Thus it appears that there are some differences between the degree of entrainment of kinematic and neuromuscular features of bilateral movements based on whether they are discrete or rhythmical, use homologous or nonhomologous limbs, are under time constraints, or differ in kinematic goals. However, exploration of kinematic and neuromuscular adjustments to asymmetric loading during discrete, identical bilateral movements of homologous limbs under the time constraint of moving the limbs simultaneously and as quickly as possible has been minimal. The overall objective of the present study was to examine the ability of the motor system to independently organize the discrete movement of both upper limbs to equidistant targets when one of the limbs is loaded under specific timing constraints. Three aims were addressed: (1) to characterize the adaptations by the loaded arm when loads of two differing magnitudes were imposed; (2) to measure whether the adaptations observed in the loaded arm impinged on the muscle activation and kinematic characteristics of the unloaded arm; (3) to examine how the strength of coupling was affected by the magnitude of the externally imposed loads.

Methods

Participants

A convenient sample of ten healthy, male university students between 22 and 26 years of age participated in the present study after signing an informed-consent form. An approval of the research procedures regarding the use of human subjects in the experiment was obtained from McGill University's Research Ethics Committee, confirming that all research procedures had been performed in accordance with the ethical standards laid down in the Declaration of Helsinki. All participants were self-declared, right-hand dominants and had no previous record of upper limb motor dysfunction.

Apparatus and task

Performers were seated behind a rectangular experimental table and the table height was adjusted so that the shoulder was level with the tabletop. The experimental task required the rapid forward projection of both arms (using elbow extension and shoulder horizontal adduction) so as to reach photo-cell targets (interconnected to LEDs) placed close to the distal end of the table surface and at a predetermined distance that corresponded to full reaching (Fig. 1). The instructions were to "move both arms as fast as pos-

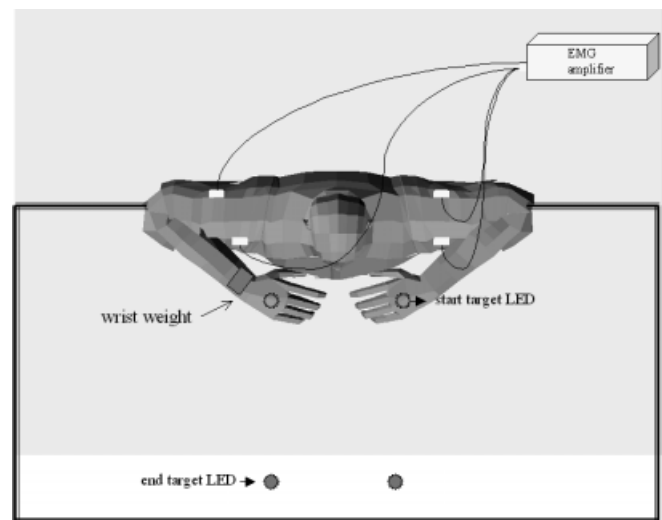


Fig. 1 A top view of the experimental apparatus and a participant. The task required the bilateral arm reaching to maximum distance targets (end-target LEDs). Two different wrist weights corresponding to a 25% and 50% increase in the inertial mass of the arm were attached to the dominant (right) arm's wrist

sible" while keeping movement time constant across both limbs. The task was performed under three conditions: one with both arms unloaded (symmetrical condition), and then two asymmetrical conditions, with an inertial load corresponding first to 25% and then to 50% of arm mass attached to the right-dominant limb with Velcro straps at the wrist. The mean arm mass of the group participating in this study was calculated to be 3.995 ± 0.62 kg (Dempster 1955; in Winter 1990). Based on this information, the first weight was set to 1 kg (25% increase in arm mass) and the second to 2 kg (50% increase in arm mass). The mean distance between the axis of rotation at the elbow and the extra weight was 22.61 ± 1.93 cm. The experiment was divided into three trial blocks ($n=10$), one symmetrical and two asymmetrical. The three sessions were counterbalanced to account for any possible order effects. Data recording for each trial started 350 ms before a computer-generated "go" signal and lasted for a total of 1.5 s.

EMG analysis

An eight-channel amplifier (Myosystem 2000; Noraxon) was used to record EMG activity of selected elbow and shoulder muscles. Surface bipolar electrodes were placed over the belly of the following muscles, with an interelectrode distance of 2.5 cm along the long axis and below the motor point of the following muscles: biceps (long head), triceps (lateral head), pectoralis major (clavicular portion), and deltoid (posterior portion). The signals were pre-amplified (gain of 1,000), band-pass filtered (cut-offs at 15 Hz and 500 Hz), and digitally sampled at a rate of 1,000 Hz. After full-wave rectification and a visual inspection of the frequency spectrum of the signals using spectral analysis, the linear envelopes of the signals were obtained by applying a low-pass digital filter (4th-order Butterworth; cut-off frequency of 20 Hz) using IRF filter design techniques. All individual EMG profiles were first plotted across the three loading conditions to allow a visual inspection and qualitative examination of the muscle activity adaptations as a result of the added load. The onset of each muscle burst was identified as the first burst that was greater than 5 standard deviations (SD) above baseline. The first point above the mean plus 5 SDs was noted. The mean baseline was calculated over a 10-ms window before movement onset. The accuracy of the computer algorithm in detecting burst onset was double-checked by an interactive procedure which allowed visual inspection of the EMG to lo-

cate the first rise of the rectified and filtered signal above baseline. Based on this information, EMG burst onset relative to movement onset and burst duration was calculated for the four muscles in each limb. The mean amplitude value (MAV) was calculated by taking the integral of the rectified and filtered EMG over the time interval defined by burst duration.

Kinematic analysis

Experimental movements were recorded using a high-speed digital camera (E.G. and G. Reticon 4256) operating at a sampling rate of 240 Hz. Reflective markers were properly fixed over the bony prominences of the wrist, elbow, and shoulder of each limb to allow the automated digitization of the selected trials. After filtering using a low-pass, 4th-order digital filter (cut-off at 5.5 Hz), the *x-y* spatial coordinates were numerically differentiated to obtain the linear and angular segment kinematics. The upper limb was modeled as a two-segment, rigid link system with frictionless joints at the shoulder and the elbow (Winter 1990). A relative velocity threshold of 10% of the maximum rotational forearm velocity was used to detect the start and the end of each movement (Boessenkool et al. 1999). The temporal parameters examined in the present study were movement time, and maximum forearm and upper arm velocity.

Statistical analysis

All EMG and kinematic variables were calculated per trial and then averaged across performance conditions. Grouped data (*n*=10) for each dependent measure were analyzed by a 3 (Load-

ing) × 2 (Arm) analysis of variance (ANOVA) with repeated measures on both factors. The first factor included the unloaded and two loaded conditions (25% and 50% of added mass), and the second factor referred to the loaded (right) versus unloaded (left) limb comparison. The Huynh-Feldt epsilon correction was used to control for the sphericity assumption. Loading by Arm interactions were further analyzed by running one-way ANOVAs on the Loading factor, separately for the loaded and unloaded arm.

Results

When the individual EMG profiles were plotted along with the kinematics across the three load conditions, a consistent kinematic profile was observed across all but one of the subjects, who seemed to adopt a slightly different movement strategy as explained below. The EMG and kinematic data of the loaded and unloaded arm for a representative individual are plotted in Fig. 2). The kinematics revealed prolonged movement duration and decreased segment velocities exclusively for the limb carrying the

Fig. 2a–d Linear envelopes of the triceps and biceps EMG activity and forearm angular velocity records plotted across the load conditions for the loaded (a, b) and the unloaded arm (c, d). Sample trial data from a representative individual are presented. EMG data have been normalized with respect to movement onset (dashed vertical lines mark movement onset)

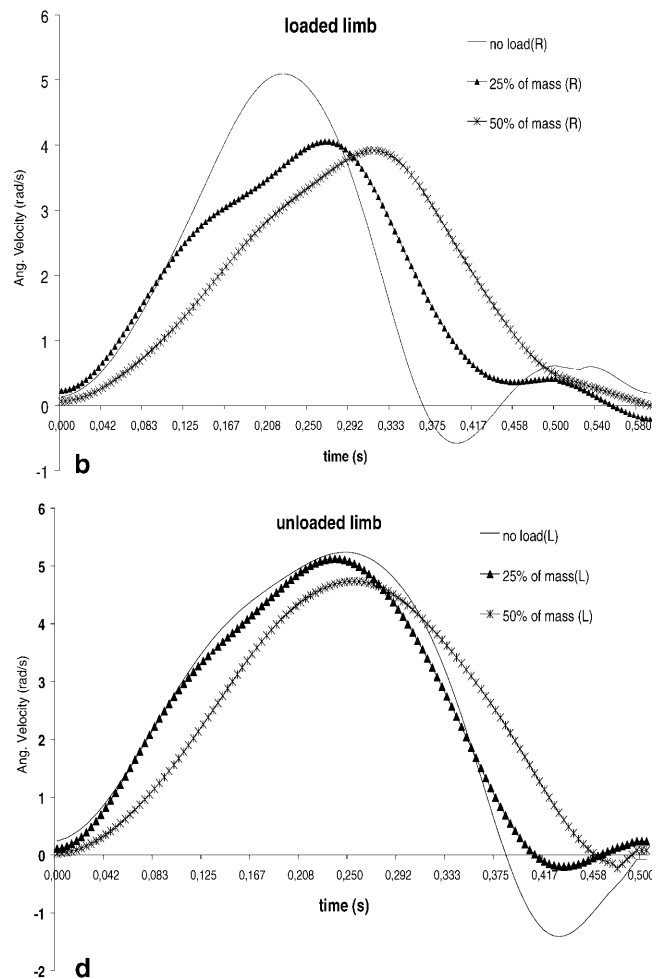
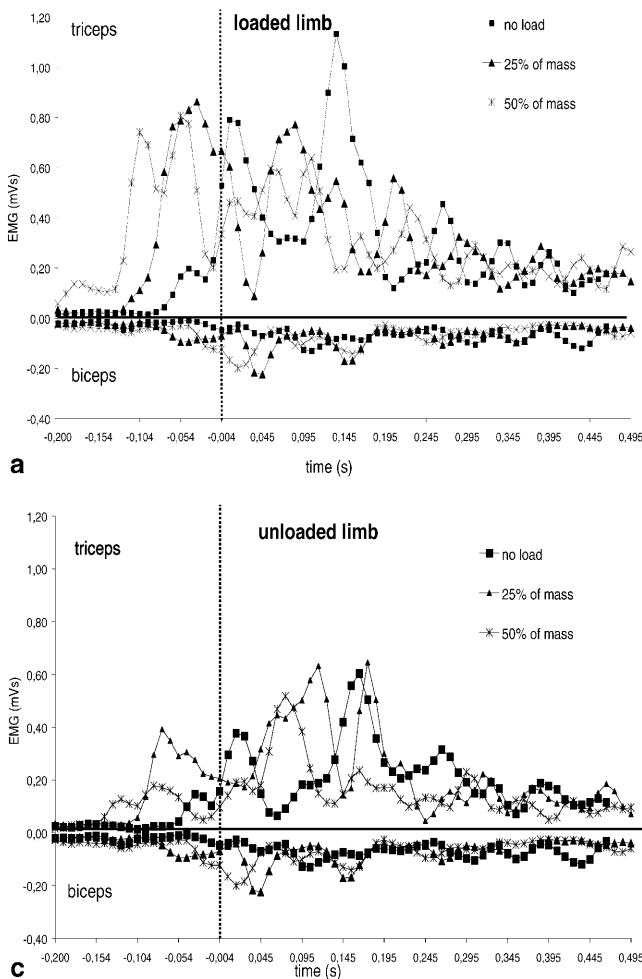


Table 1 Means ($n=10$) and standard deviations for movement time and segment angular velocity calculated for the loaded and unloaded arm across conditions

Load	Loaded arm (right)						Unloaded arm (left)					
	0		25%		50%		0		25%		50%	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Movement time (ms)	0.378	0.098	0.451	0.091	0.470	0.064	0.380	0.092	0.406	0.105	0.398	0.086
Forearm	5.43	1.25	4.63	1.05	4.15	0.920	5.49	1.31	5.17	1.28	5.04	1.21
Upper arm angular velocity (rad/s)	4.26	0.68	3.69	0.63	3.20	0.54	4.23	0.75	4.16	0.75	4.04	0.87

Table 2 Means ($n=10$) and standard deviations for the EMG parameters calculated for the loaded and unloaded forearm across conditions

Load	Loaded arm (right)											
	Triceps						Biceps					
	0		25%		50%		0		25%		50%	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Rel. burst onset (ms)	-60.10	76.3	-119.8	43.9	-84.0	49.52	48.9	111.8	11.8	91.02	-3.1	94.3
EMG burst duration (ms)	374.70	111.2	482.30	116.2	544.10	97.65	331.30	111.31	372.40	93.31	502.80	195.42
MAV (mV/ms)	0.4368	0.17	0.3842	0.198	0.3769	0.183	0.2024	0.095	0.1535	0.046	0.1406	0.062
Load	Unloaded arm (left)											
	Triceps						Biceps					
	0		25%		50%		0		25%		50%	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Rel. burst onset (ms)	-72.8	50.65	-111.1	54.75	-77.2	32.18	43.8	81.2	-6.4	84.6	40.8	56.9
EMG burst duration (ms)	411.70	88.93	492.00	106.2	476.00	62.47	340.80	105.9	375.30	126.8	369.20	109.0
MAV (mV/ms)	0.3658	0.133	0.3354	0.105	0.3386	0.129	0.1607	0.0039	0.1378	0.053	0.1144	0.036

extra load (see Fig. 2b). By contrast, the kinematic profile of the unloaded limb (Fig. 2d) remained invariant across loading, with the exception of a single performer who displayed increased peak velocities in the unloaded limb due to contralateral limb loading. While the pattern of EMG activity observed across the different participant profiles was less consistent, common characteristic responses were observed across all participants. These characteristic EMG activity patterns for the different load conditions of a representative subject are illustrated in Fig. 2a–c. The means and standard deviations for all dependent measures are presented in Tables 1, 2, 3.

Kinematics

A highly significant main effect of Arm ($F_{1,9}=29.07$, $P<0.001$) on movement time confirmed that there were significant differences in movement duration between the two arms, suggesting that the right arm required a longer time period to complete the movement than the left arm. The analysis also revealed a significant Loading by Arm interaction ($F_{2,18}=11.85$, $P<0.01$). To further analyze this interaction, one-way ANOVAs were run on the loading factor (3 levels) for each arm separately. The analyses revealed a significant effect of Load on the movement time of the right arm ($F_{2,18}=6.62$, $P<0.01$), while the movement time for the left arm was not significantly affected by loading ($P>0.05$). Mean movement duration for the right arm increased from 378 ms to 451 ms and 470 ms with the addition of the

Table 3 Means (n=10) and standard deviations for the EMG parameters calculated for the loaded and unloaded upper arm across conditions

Load	Loaded arm (right)						Unloaded arm (left)					
	Pectoralis						Deltoid					
	0		25%		50%		0		25%		50%	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Burst onset (ms)	-16.49	86.3	-40.64	97.8	-52.57	85.6	-69.28	16.8	-53.06	23.7	-64.37	20.0
EMG burst duration (ms)	432.3	51.4	513.6	139.3	513.1	146.8	380.9	77.7	457.2	128.2	497.6	99.3
MAV (mV/ms)	0.2305	0.066	0.2122	0.089	0.2136	0.065	0.2396	0.242	0.1972	0.128	0.1987	0.148

Load	Unloaded arm (left)											
	Pectoralis						Deltoid					
	0		25%		50%		0		25%		50%	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Burst onset (ms)	-27.98	84.7	-42.61	102.5	-26.29	83.5	-69.18	38.5	-57.62	65.1	-64.05	42.1
EMG burst duration (ms)	431.9	79.3	509.2	131.4	506.2	117.8	327.4	80.09	450.2	187.2	432.7	162.6
MAV (mV/ms)	0.2707	0.145	0.2548	0.106	0.2381	0.127	0.2394	0.175	0.2156	0.151	0.1726	0.112

25% and 50% load, respectively, whereas it remained relatively constant across all loading conditions for the left arm (Table 1).

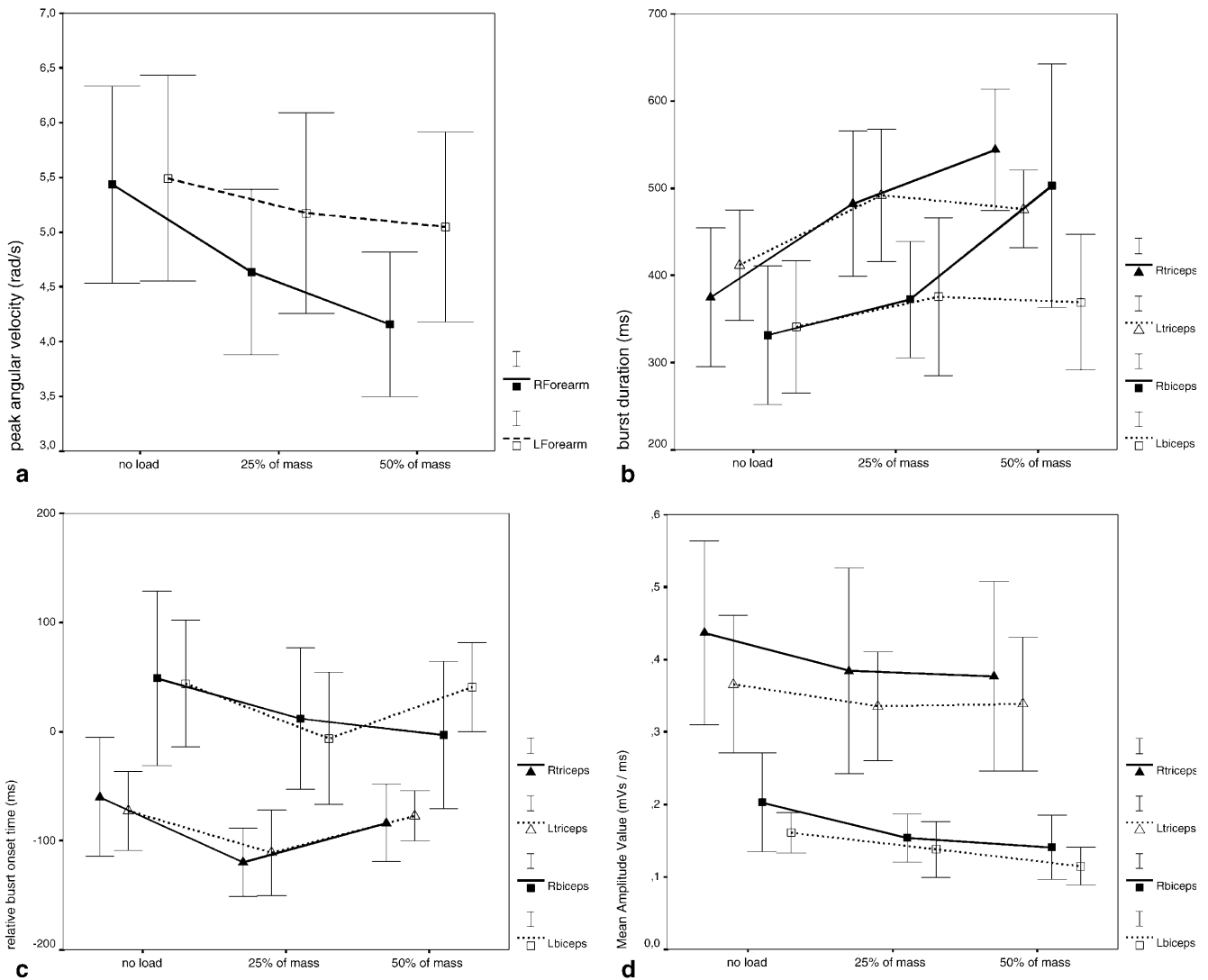
Concomitantly, highly significant main effects of Arm on peak angular velocity of both the forearm and upper arm ($F_{1,9}=20.67$, $P<0.01$; $F_{1,9}=21.37$, $P<0.01$) were observed. In addition, a significant Loading by Arm interaction for both the forearm ($F_{2,18}=19.54$, $P<0.001$) and upper arm ($F_{2,18}=29.7$, $P<0.001$) peak angular velocity suggests that the loading procedure slowed down the movement of the right arm but did not affect the movement of the left arm (see Figs. 3a, 4a). Post hoc one-way ANOVAs were performed separately on the loaded and unloaded arm and these analyses revealed a significant decrease in the peak angular velocity for both the forearm ($F_{2,18}=13.79$, $P<0.001$) and upper arm ($F_{2,18}=24.84$, $P<0.001$) of the loaded limb. This decrease was linearly scaled to the magnitude of the extra load, suggesting an inverse relationship between the mass attached to the arm and its reaching velocity. On the other hand, segment velocities of the left-unloaded arm remained relatively constant across the loading conditions, as confirmed by a nonsignificant change for peak forearm ($P>0.05$) and upper arm ($P>0.05$) angular velocity.

Elbow EMG characteristics

Burst duration

For the triceps, the ANOVA indicated a significant main effect of loading ($F_{2,18}=5.045$, $P<0.05$) but not of the arm ($P>0.05$). In addition, a significant Loading by Arm interaction was found ($F_{2,18}=8.48$, $P<0.01$), suggesting that the right-left difference in burst duration was dependent on the level of loading (see Fig. 3b). Interaction breakdown revealed that triceps burst duration was significantly prolonged for the right-loaded arm at both the 25% and 50% load condition ($F_{1,9}=5.59$, $P<0.05$ and $F_{1,9}=9.02$, $P<0.05$, respectively). Burst duration of the triceps of the left-unloaded arm was also significantly increased as a result of the 25% extra load from 411 ms to 492 ms, indicating a coupling effect ($F_{1,9}=4.95$, $P<0.05$). However, a ceiling effect was also observed in this arm, as further increase in the load to 50% did not significantly prolong burst duration ($P>0.05$).

By contrast, for the biceps, a significant main effect of Arm on burst duration ($F_{2,18}=7.22$, $P<0.05$) was noted, suggesting that burst duration was significantly different between the limbs. The main effect of Load on burst duration and the Loading by Arm interaction reached marginal significance ($F_{2,18}=3.41$, $P=0.056$; $F_{2,18}=3.46$, $P=0.053$), suggesting that the loading procedure tended to affect burst duration in one of the two arms



(see Fig. 3b). The post hoc contrast analysis revealed that burst duration for the right biceps was significantly prolonged ($F_{2, 18}=5.25$, $P<0.05$) but was specifically due to the 50% load (of extra mass) condition ($F_{1, 9}=8.98$, $P<0.05$), as the smaller load (25% of extra mass) was not sufficient to prolong significantly burst duration. However, left biceps' burst duration was not affected by contralateral limb loading ($P>0.05$).

Burst onset

For the triceps, a significant main effect of Loading was found ($F_{2, 18}=4.19$, $P<0.05$), but no significant main effect of Arm or interactions ($P>0.05$). Post hoc one-way ANOVA tests run separately on each arm confirmed that increasing the mass of the dominant-right arm by 25% resulted in a significantly earlier burst onset of the triceps in both arms relative to movement onset (right limbs: $F_{1, 9}=5.53$, $P<0.05$; left limb: $F_{1, 9}=4.12$, $P<0.05$), suggesting a coupling effect in the 25% load condition (see Fig. 3c). However, further increase in the load to

Fig. 3a–d Peak forearm angular velocity (**a**), triceps and biceps burst duration (**b**), relative burst onset (**c**), and mean amplitude value (**d**) plotted for the loaded (*continuous line*) and the unloaded (*dashed line*) arm across the three loading conditions. *Filled symbols* represent loaded limb; *empty symbols* represent unloaded limb; **b–d triangles**, agonist muscle; **squares**, antagonist muscle

50% of the arm mass did not result in an analogous shift in triceps onset ($P>0.05$), revealing a ceiling effect in the 25% load condition for the loaded limb, and a return to the onset time observed for the unloaded condition in the unloaded limb (see Fig. 3c). Burst onset of the biceps was not affected by single-limb loading, as there were no significant main effects of either Loading or Arm on this parameter and there was no significant interaction ($P>0.05$). However, a slight tendency of the biceps onset to occur earlier with respect to movement onset as a result of the added load was noted in both limbs (see Fig. 3c).

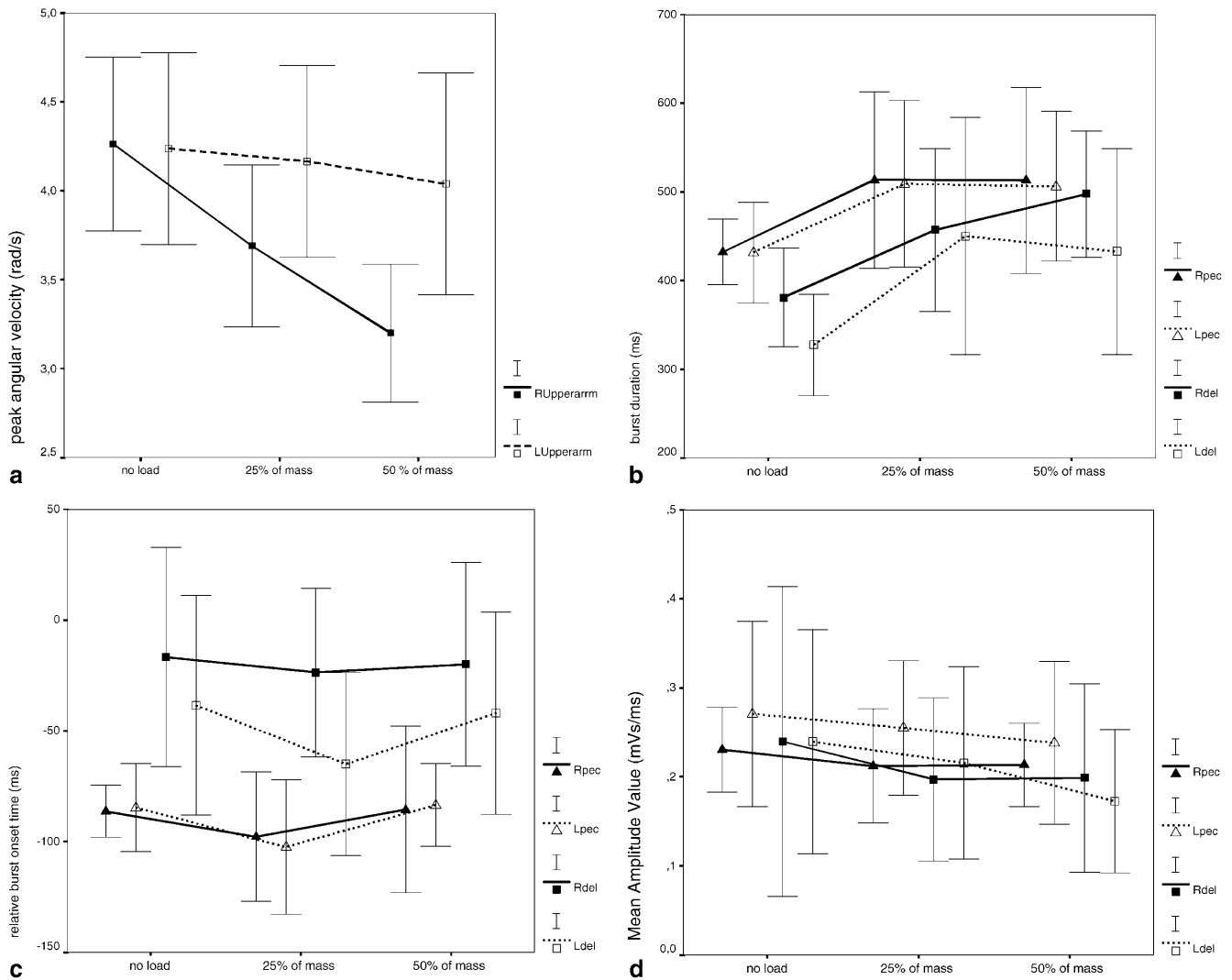


Fig. 4a-d Peak upper arm angular velocity (a), pectoralis and deltoid burst duration (b), relative burst onset (c), and mean amplitude value (d) plotted for the loaded (*continuous line*) and the unloaded (*dashed line*) arm across the three loading conditions. Conventions as in Fig. 3

Mean amplitude of EMG activity

There were no significant main effects or interactions for the triceps (Fig. 3d) for this aspect of single-limb loading ($P > 0.05$). By contrast, the MAV of the biceps decreased significantly as a result of the main effect of Loading on biceps MAV ($F_{2, 18} = 6.44$, $P < 0.01$). The post hoc contrasts indicated that this decrease was highly significant only at the 50% ($F_{1, 9} = 22.01$, $P < 0.01$) and not in the 25% ($P > 0.05$) loading condition. Biceps amplitude of EMG activity was similarly reduced in the contralateral-left limb (see Fig. 3d), as this was confirmed by a highly significant post hoc contrast for the left biceps MAV value at the 50% load loading condition ($F_{1, 9} = 11.21$, $P < 0.001$).

Shoulder EMG characteristics

Shoulder muscle parameters were less affected by loading (Fig. 4b-d). Burst duration of the pectoralis increased from 432 ms to 513 ms as a result of adding the 25% extra mass to the distal end of the dominant arm, and this increase was confirmed by a significant post hoc contrast ($F_{1, 9} = 8.72$, $P < 0.05$) of the Loading factor on burst duration. However, further increase in the load to 50% was not accompanied by a similar increase in burst duration ($P > 0.05$), again revealing a ceiling effect in the 25% load condition (see Fig. 4b). When a post hoc one-way ANOVA was run on the unloaded limb, a significant contrast in the 25% load condition ($F_{1, 9} = 5.15$, $P < 0.05$) confirmed that single-limb loading had a similar impact on the homologous muscle of the unloaded arm, indicating that agonist burst duration could not be differentially scaled between the two limbs. On the other hand, burst duration of the deltoid was differentiated between the limbs as a result of the loading, a finding that was confirmed by a significant main effect of Arm on burst duration ($F_{1, 9} = 6.97$, $P < 0.05$). A marginally significant main effect of Loading on burst duration ($F_{2, 18} = 3.21$, $P = 0.064$) and a nonsignificant

cant Loading by Arm interaction suggests that deltoid burst duration increased only in the right arm carrying the extra weight (see Fig. 4b). Mean burst duration for the deltoid increased from 381 ms to 457 ms and 497 ms as a result of adding a 25% and 50% extra mass to the right wrist, respectively. The left deltoid burst duration demonstrated a tendency to increase in the 25% load condition (from 327 ms to 450 ms), although this increase was not statistically confirmed, most likely because of the large intersubject variability in this parameter (see Fig. 4b).

Burst onset and amplitude of EMG activity

These parameters were invariant in both the pectoralis and deltoid muscles across changes in load (Fig. 4c, d), and this was confirmed by the absence of significant main effects of Loading and Arm on the EMG parameters as well as the absence of any significant interactions.

In summary, the kinematic parameters between the two limbs were uncoupled; the addition of an inertial load to the right limb resulted in an increase in movement time and concomitant decrease in peak velocity of its upper and forearm but not the contralateral arm. These adjustments were scaled to the added weight. Some degree of coupling was observed for the EMG parameters, but not in both asymmetric loading conditions. Adjustments to the inertial load on the ipsilateral limb were primarily characterized by an increase in burst duration of all muscles, with changes in activity and onset time that were load-specific: the biceps demonstrated a decrease in activity with the 50% load, and the triceps had an earlier onset with the 25% load. Concomitant adjustments on the unloaded limb consisted primarily of an increase in burst duration of the pectoralis and triceps, an earlier triceps onset solely with the 25% load and a decrease in activity of the biceps solely with the 50% load.

Discussion

The present study examined the ability of the motor system to independently organize the discrete movement of both upper limbs to equidistant targets when one of the limbs was loaded under specific timing constraints. Limited coupling between the unloaded and the loaded limb was found at the neuromuscular level but not the kinematic level, where the movements were temporally decoupled. Since the goal of the task was to achieve simultaneity in arrival at equidistant targets while executing the movement as quickly as possible, performers were not successful in achievement of the time requirement for the limb carrying the extra load. This inability could be due to the selection of a control strategy in the loaded limb that did not fulfill the time requirement, although it afforded limited decoupling between the neuromuscular adjustments in the two limbs. Alternatively it could simply be related to the effect of the inertial load on the limb and on the biomechanic properties of the

musculature. The first interpretation is suggestive of active strategy specification, while the second is suggestive of a reactive process related to the biomechanic characteristics of the system. These issues are explored further in the light of the present findings.

Interlimb organization as an active selection of movement strategy

The observation that addition of an extra mass slows down the loaded limb has also been noted under unilateral task performance (Gottlieb 1993; Gottlieb et al. 1989). Cooke and Brown (1994) and Gottlieb (1996) have further hypothesized that, when movement time is not experimentally controlled or constrained at submaximal levels, performers respond to an increase in inertial load by prolonging the duration of the EMG agonist burst. This duration modulation of the agonist EMG burst is particular to joint excursions greater than 30° (Pfann et al. 1998). Moreover, their study demonstrated that, depending on movement amplitude, a transition from a constant duration to a duration modulation of the agonist burst occurs, and this transition will occur at a shorter distance under increased inertial loading conditions. Our data indicate that prolonged burst duration and earlier burst onset are also mechanisms that the system uses to accommodate additional weight under maximum speed conditions for full joint excursion. Thus, this strategy seems to be a typical way in which performers adapt to unilateral inertial loads of large joint excursions, whether the task to be performed involves one or both of the upper extremities, and whether or not there is a time constraint on the movement.

Open- versus closed-loop control

The observed temporal coupling in the agonists might be attributed to premovement control processes that regulate agonist activity in an open-loop fashion based on established or planned descending commands. It might be argued, therefore, that interlimb interference is due to the interaction of preset descending commands that are prepared before afferent information is available, since these phenomena occur before the onset of any observable movement (Swinnen et al. 1994). This notion has been further supported by experimental evidence showing that interference between the limbs during dual-task performance can occur in spite of the absence of proprioceptive information and can therefore be attributed to movement planning or organization (Teasdale et al. 1994). Other studies have also provided evidence that interference occurs before the onset of the movement in the form of burst onset synchronization of the homologous agonist muscles of the two limbs (Hatzipati and McKinley 1998; Serrien and Swinnen 1998) or in reaction time measures (Garry and Franks 2000; Heuer 1991). These findings may provide a possible explanation for the overflow effect observed in the contralateral limb musculature in the

form of a prolonged burst duration in the agonists and an earlier triceps onset in the unloaded limb.

On the other hand, the differentiation in burst duration of the movement antagonists between the loaded and unloaded limb may be the result of postinitiation kinesthetic afferent processes. This hypothesis is supported by experimental evidence suggesting that the nervous system exploits the incoming sensory information from the moving limbs in order to compensate for asymmetric load perturbations (Baldissera et al. 1991; Peper and Carson 1999; Serrien and Swinnen 1998). Indeed, Sittig et al. (1987) have proposed that velocity feedback in moderately fast movements may play a crucial role in the brake time of said movements; thus the difference in peak velocity experienced at the two limbs may have provided cues to permit uncoupling of this parameter. These adaptations may be attributed to the presence of pathways in the upper limb that mediate crossed-reflex effects by means of afferent feedback arising from movement or load-elicited discharge of somatosensory receptors (Peper and Carson 1999; Swinnen et al. 1994).

This interpretation seems to also agree with the three-element model proposed by Gottlieb (1996), and it addresses how the CNS compensates for inertial loading. According to this model, for fast movements performed under predictable load conditions such as the ones examined in the present study, the α command, which centrally specifies the muscle activation patterns that will produce the desired trajectory, is usually accurate and adequate to perform the task. Based on the present findings, it might be suggested therefore that α command centrally specifies the duration of the agonist burst according to the expected load requirements, and this modulation is common in both limbs. On the other hand, the λ component would contribute little in this case, because the comparison of the kinematic reference plan to the input sensory signals requires the use of a feedback mechanism that takes place only in relatively slow movements, usually against unpredictable loads. Thus, in the present paradigm no such neuromuscular compensations due to a kinematic drive would be possible because of the maximum speed constraint imposed on the movements.

As found with previous studies (Hatzitaki and McKinley 1998; Marteniuk et al. 1984; Sherwood 1990, 1991; Walter and Swinnen 1990), coupling strength of the agonists was dependent on the magnitude of the interlimb asymmetry, being greater at 25% than at 50% loading; performers were better able to differentially scale burst duration between the limbs in the 50% load condition. The increase in burst duration, however, was accomplished in two ways. First, burst onset occurred earlier in both the 25% and 50% conditions; secondly the offset was delayed in the 50% condition. Thus, there may exist a specific time limit for when the triceps can be activated, as this earlier onset is the same for both the 25% and 50% weights (ceiling effect at 25%). Further, dissociation of muscle burst duration between the limbs for the 50% weight occurred because increase in triceps burst duration was a function of delaying the burst offset, but only in the

loaded limb. It might be argued therefore that burst offset can be differentially scaled between the limbs because it is regulated by a closed-loop feedback mechanism.

Modulation characteristics are selected to avoid entrainment

We hypothesize that, in order to accomplish to the best of its ability the asymmetric loading task with time constraints, the nervous system attempted to avoid entrainment by specific selection of EMG characteristics that were modulated. This selection, while demonstrating limited coupling, was able to make use of kinesthetic feedback to differentially scale some temporal aspects of the EMG signal. One outcome of this strategy, however, was the lack of fulfillment of the instruction to arrive at the end point simultaneously. Clearly, increased duration and earlier onset (pulse width adjustment), without increased activity (pulse height adjustment) in the agonist muscles, were unsuccessful modulations for accomplishing this requirement in the loaded limb. On the other hand, successful and simultaneous arrival of both limbs to the end target LEDs under maximum speed conditions would indicate that performers could differentially scale the muscle activity patterns between the limbs in such a way as to achieve the constant movement time requirement. Yet no increase in EMG activity was observed in the loaded arm. It is possible that this option did not occur because the task was performed with full recruitment of agonist muscle motor units. Indeed, Hoffman and Strick (1993) have reported that, when the force output cannot be augmented by increasing the peak amplitude of the EMG burst, the additional force is generated by increasing burst duration. On the other hand, Pfann and colleagues (1998) have suggested that modulation of agonist burst duration during unilateral loading is not necessarily due to a saturation phenomenon. By contrast, burst duration modulation may occur even when the force requirements of the task do not exceed those that can be generated by amplitude modulation. Thus in the paradigm of asymmetric loading, it might be too difficult to increase the amount of activity voluntarily in the agonist of the loaded arm without doing the same with the other arm, and the lack of increase in activity might be an attempt to minimize crossover effects to the nonloaded arm.

Alternatively, asking performers to simultaneously arrive at the end targets could have induced a reduction in EMG activity of nonloaded limb muscles, thus resulting in a slower movement of the nonloaded arm. Since this did not occur, one could argue that not only did subjects attend to the given instructions to move "as quickly as possible" but they also avoided activity modulation as a means of satisfying the requirement of simultaneity. This avoidance of activity modulation might have served not only to minimize entrainment at the neuromuscular level, but also to minimize kinematic differences between the loaded and unloaded arms. Even though the unloaded arm showed limited coupling in modulation of the temporal characteristics of agonist EMG, the nonloaded left limb

did not move faster than in the no-load condition. Thus, this modulation strategy also affords some tolerance at the kinematic level. These differential effects of loading on movement kinematics and muscle activation characteristics has been attributed to joint-compliant properties revealed by the length-tension and force-velocity properties of the muscles that minimize the effects of external load changes on the kinematic trajectory (Gottlieb 1993).

Interlimb organization: a reactive process attributed to task constraints or limb biomechanics

The inability of performers to achieve simultaneous arrival to the end targets by differential scaling of the EMG amplitude can also be a consequence of the task dynamics in relation to the biomechanical properties of the system. In rhythmical movement tasks such as bilateral tapping, the involved effectors maintain their strong interlimb synchronization across perturbations (Scholz and Kelso 1990), irrespective of unilateral loading (Kelso et al. 1979; Serrien and Swinnen 1998), changes in stiffness (Baldissera et al. 1991; Bingham et al. 1991), or variations in the level of isometric activation of one limb (Peper and Carson 1999). It should be noted, however, that such rhythmical tasks most frequently involve small-amplitude, single-joint movements of distal appendages with small inertias. On the other hand, when the oscillating bilateral pattern involves movements of greater amplitude, or multijoint effectors with different inertial characteristics, temporal assimilation between the limbs is substantially reduced (Jeka and Kelso 1995). Zelaznik et al. (2000) have suggested that demands for temporal integration or assimilation are high for small-amplitude movements, but decrease with larger movement amplitudes. Based on this evidence, it seems reasonable to suggest that constraints such as inertial characteristics of the involved effectors, movement amplitude, and number of involved joints may strongly impinge on the temporal organization of the bilateral task and explain why simultaneity in target arrival was not possible under the present task conditions.

Another example of how the task dynamics of a three-segment system may influence interlimb organization relates to the reduction of the biceps activity noted in both limbs when the load increased to 50% of the arm's mass. It has been shown that, during arm reaching under no-loading conditions, the amount of force necessary to brake the limb movement and bring the limb to a halt during the deceleration phase is provided by the interactive, passive forces acting on the forearm due to the inertial influence of the upper arm (Hatzitaki and McKinley 1998). Thus, inertial influences generated by segment interactions minimize the need for active muscle involvement in the braking process. Increasing the inertial mass of the limb by adding a weight equal to 50% of the arm's mass to its distal end is expected to enhance the passive contribution of the interactive forces in the braking process and therefore minimize the need for active biceps

participation even further. This finding is also in agreement with previous studies which have reported that the antagonist EMG burst scales with inertial loading in accordance with the torque requirements for braking the movement (Gottlieb et al. 1989; Karst and Hasan 1987; Lestienne 1979; Pfann et al. 1998).

Individual variability

Finally, it must be noted that some of the EMG adaptations observed when plotting the grouped muscle parameters were not found to be statistically significant. This lack of significance may be due to the highly variable nature of characteristics such as burst onset or EMG amplitude across different subjects. It seems possible that performers may have chosen their own, subject-specific strategy to compensate for the extra load. This highly variable and individualized nature of the EMG responses to the added load, as pointed by other investigators (Gottlieb 1996; Pfann et al. 1998), suggests that each participant selects his own very specific strategy to compensate for the extra load. Another source of interindividual differences is the degree of interlimb dependency. Electrophysiological studies have reported considerable individual differences in the degree of coupling or dependence between limb movements (Peters 1985; Swinnen et al. 1988). This means that in some performers the movements of both limbs are highly linked dynamically, while others display more independent limb movements. In the present study, a visual inspection of the EMG signals of both the loaded and unloaded arm allowed us to note that the effect of limb loading on the muscle activation characteristics of the contralateral limb was also subject-dependent.

In summary, the present study examined the ability of the motor system to independently organize the discrete movement of both upper extremities to the same target when asked to move as quickly as possible but when carrying different inertial loads. Prolonged burst duration and an earlier burst onset seem to be the mechanisms used by the system to accommodate for the extra load under maximum speed conditions. Limited coupling between the unloaded and the loaded limb was found at the neuromuscular level but not the kinematic level, where the movements were temporally decoupled. On the other hand, performers were unsuccessful in meeting the time constraint requiring simultaneous arrival of both limbs to the end target. This inability can be the result of an active strategy selection to safeguard the actions against interference or, alternatively, it could simply be a consequence of the system's biomechanical properties in relation to task constraints.

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