

Goal-directed Arm Movements. III: Feedback and Adaptation in Response to Inertia Perturbations

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Summary: Goal-directed shoulder-elbow movements with a maximal and with a submaximal velocity have been studied. At the movement onset the inertial load to be displaced was changed unexpectedly. The adaptation of movement and muscular activity have been described with a moving average model. Significant adaptation effects were demonstrated in the first two or three movements after a change of mass. Adaptation only partly compensated the mass effects: A higher mass led to a persistent reduction of movement velocity. Amplitudes of muscular activity showed no adaptation of muscular effort, but activation durations were strongly modified. Thus the hypothesis that adaptation pursues a certain movement trajectory as a function of time had to be rejected. However, after scaling towards peak velocity, a shape invariance was demonstrated in the movement trajectory. In the first movements after a change of mass, effective and substantial modifications of muscular activity appeared about 90 ms after movement onset. Earlier modifications suggest a force feedback leading to a yielding towards the disturbance instead of a compensation. Such force feedback may, however, increase system bandwidth as it will allow increased position/velocity feedback gains. **Key Words:** Feedback—Adaptation—Kinematics—Shape invariance—Electromyography.

This paper concerns goal-directed movements in changing conditions. We will study both feedback and adaptation. Feedback will be defined as a direct effect of sensory information on neural inputs, whereas adaptation has an indirect effect, also affecting behaviour in future movements. (This definition of adaptation partially overlaps common definitions of learning.) A plausible interpretation of adaptation is that an internal representation exists in the central nervous system containing

knowledge of the task, the environment and the body²⁹. Sensory information will be used to adapt the internal representation. This internal representation will then be used to adjust the control strategy.

That proprioceptive information affects muscular activity in fast goal-directed movements is demonstrated by perturbation experiments^{7,26,27,31} and by tendon vibration experiments^{10,18}. Jeanerod and Prablanc¹⁹ state that the presence of visual information contributes to the accuracy in arm movements lasting longer than 250 ms. These observations indicate that feedback is also effective in fast movements. However, due to neural delays, the first phase of fast movements is unaffected by sensory information and is thus under open-loop

Accepted January 22, 1993.

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control. This open-loop phase is about 100 ms in arm movements³¹. This is substantial as durations of arm movements can be as low as 150 ms.

The human arm can control objects of much larger weight than the arm itself. It is obvious that an open-loop control should be adapted to the mass to be displaced. Also, it may be necessary to adapt feedback parameters such as to maintain stability and a reasonable performance. Often in daily life objects of which the mass is not accurately known have to be displaced. So, the displacement of an unknown mass is a realistic movement condition in which adaptation and feedback effects can be expected.

Movement kinematics are found to have invariant characteristics or a shape invariance in certain limited conditions^{4,5,23,24,28}. Position, velocity and acceleration traces as a function of time are reported to have an identical shape for movements of a different amplitude and/or velocity or even direction³. The shape is invariant; but duration and amplitude are scaled to match the movement objective. This concept has also been linked to actual control schemes; it is then assumed that the standard trajectory is a time-dependent desired position/velocity which is attained by low level feedback possibly combined with open-loop control²⁴. In changing conditions the goal of adaptation can be to retain the desired trajectory. The current paper focuses on the goal of adaptation in terms of shape-invariance. A second aspect studied is the temporal course of adaptation and whether feedback and adaptation can be separated in time. Both maximally fast and relatively slow movements will be considered. In maximally fast movements, inputs are (near-) maximal. Due to this constraint, certain adaptation goals may not be reached. In slower movements, a more complete adaptation is to be expected.

METHODS

Experiments

After being fully informed about the experiment four healthy male subjects (average age 23 years) volunteered to participate in the study. All, except one subject showed right-side dominance. The subjects were naïve with respect to the research aims and the nature of the load disturbances.

With their right hands the subjects controlled a manipulator with one degree of freedom; a forward

or backward movement of the hand. The arm was in the sagittal plane, with a roughly horizontal forearm¹². Both the displacement of the manipulator and the target position were presented on a display. The manipulator was built as a linear electro-hydraulic servomotor which has the characteristics of a damped mass-spring system. The parameters of the manipulator can be varied over a large range. A more elaborate description of the set-up can be found in^{12,22}. In the experiment, the target jumped to a new position after random time intervals. In this way, a step tracking task resembling a goal-directed movement was executed. A stepsize of 0.2 metre was chosen, and both forward and backward movements were recorded. Visual feedback was continuously present during movements, thus providing a natural condition for adaptation. At the onset of some movements the virtual mass to be displaced was unexpectedly changed. The movement onset was detected from the force exerted by the hand on the manipulator. The mass change was effected through the electro-hydraulic servomotor with a time constant of 2 ms. The mass was changed from 0.6 to 5.6 kg or back to 0.6 kg. Thus two conditions and two transitions (a rise or drop of mass) were studied. The sequence of mass as a function of the movement number was generated with a random generator. It was ensured that the sequence had a zero correlation between mass and movement direction and a negligible mass auto-correlation over three movements. The random generator was run a few times until the sequence met these conditions. Between one and five subsequent movements were performed with the same mass. This is acceptable, as previous research showed that adaptation processes are observable only in a few movements after the change of the movement condition. This procedure has the advantage that a large number of transitions is studied in one experimental run. This is very important, as adaptation effects are of the same order of magnitude as the natural variability²³.

Using verbal feedback, subjects were first trained to make movements with a varying mass with a peak velocity of about 0.8 ms^{-1} . Then 100 movements with varying mass were recorded at this moderate velocity. Thereafter a similar run was performed with the instruction to move maximally fast. Finally, 30 movements with a constant low mass and 30 movements with a high mass were recorded with a maximal movement velocity.

Range effects cannot be avoided in such exper-

iments; subjects can execute their tasks in a way adapted to intermediate values within the range of expected conditions, although in this experiment a task with intermediate conditions was never executed. In this task, the possibility exists that subjects recognize the two mass conditions and switch to a prepared program thus reducing the adaptation task to a recognition and switching task. However, the subjects appeared not to be aware of the fact that only two conditions occurred. The experiments with a constant mass were executed to determine in how far the behaviour depended on the uncertainty of the mass.

Data Collection

The surface electromyographic activity (EMG) of 12 shoulder muscles (or muscle parts) of which the biceps brachii also spans the elbow was recorded (Table 1). This large number of muscles was studied to gain insight into the coordinated control of shoulder muscles. Most muscles were studied in all subjects. However, some muscles were not studied in all subjects and in some cases the data were discarded because of movement artifacts. The resulting number of subjects per muscle is shown in Table 1. Bi-polar EMG recordings were obtained with disposable Ag/AgCl electrodes with an inter-electrode distance of 23 mm directly attached to a pre-amplifier. The signals were bandpass filtered from 20–1500 Hz, rectified and low pass filtered (100 Hz). These EMG signals were sampled at 250 Hz, together with the position and velocity of the hand and the force exerted by the hand.

Data Analysis

In the EMG records of goal-directed movements, three relevant phases can be found^{2,4,12,20,31}. Agonist activity in the first phase causes acceleration of the limb. Antagonist activity in the second phase serves to decelerate the limb. The agonist activity in the third phase is shown to be relevant in fast movements^{8,9,32}. The third phase is required for a time optimal movement where it serves to compensate the slowly decaying antagonist force¹¹.

From the EMG records, the timing and the average amplitude of the three phases were determined. This was done per movement and per muscle using a statistical detection method¹². Parameters are defined in Table 2. In Happee¹³ a method to analyse movement kinematics (position, velocity trace) has been presented. From the kinematics, five parameters can be estimated. Four parameters describe a triphasic input pattern. These parameters correlate highly to the relevant EMG parameters. A fifth parameter represents neuromuscular dynamics. These five parameters are defined in Table 2 where parameters scaled to movement peak velocity V_{max} are also defined. The scaled parameters provide a means to compare the shape of movement traces under different experimental conditions.

Thus the EMG and the kinematic signals are described by two sets of parameters (Table 2). By means of a linear multiple regression, a dynamic model is made of the response to a changing mass for these parameters. The regressors used are given in Table 3. A static effect of mass is described by the regressor M which is the mass in the current

TABLE 1. *Muscles and functions as apparent from EMG patterns*

Muscle	(Subjects)	EMG	Remarks
trapezius pars descendens	(3)	?	scapular muscle
trapezius pars transversalis	(2/3)	- ag	scapular muscle
trapezius pars ascendens	(3)	?	scapular muscle
serratus anterior	(4)	+	scapular muscle
infraspinatus	(3)	both	rotator cuff muscle
deltoideus pars anterior	(4)	+	prime mover
deltoideus pars media	(3)	?	prime mover, abductor
deltoideus pars posterior	(4)	-	prime mover
latissimus dorsi	(4)	-	prime mover
pectoralis major pars clavicularis	(4)	+	prime mover
pectoralis major pars thoracalis	(4)	+	prime mover
biceps brachii	(3)	- con	bi-articular; shoulder elbow

+, contributing to a forward force, or acceleration; -, contributing to a backward force, or acceleration; ag, only clear as agonist, not as antagonist in other movement direction; con, continued activity during agonist and antagonist phase; both, in both directions agonist activity is found; ?, function not clear; (subjects) = number of subjects for which EMG records of this muscle are available; two values (x/n) indicate that the reported function is found in x out of n subjects.

TABLE 2. Parameters estimated from EMG and kinematic records

EMG, evaluated for each muscle separately as described in Happee ¹²	
T_d	delay from stimulus to first activity
T_a	duration first phase (agonist)
T_b	duration second phase (antagonist)
T_c	duration third phase (agonist)
A_a	amplitude first phase (agonist)
A_b	amplitude second phase (antagonist)
A_c	amplitude third phase (agonist)
Kinematic parameters, estimated as described in Happee ¹³	
V_{max}	peak velocity
T_{dk}	delay from stimulus to movement
T_{ak}	duration first phase (agonist)
T_{bk}	duration second phase (antagonist)
T_1	neuromuscular time constant
R_c	magnitude of the third phase relative to the first phase
T_{aks}	$T_{ak} V_{max}$
T_{bks}	$T_{bk} V_{max}$
T_{ls}	$T_1 V_{max}$

index: k = kinematic; s = scaled to movement peak velocity V_{max} .

movement. Adaptation is modelled with the moving average regressors DM_i with $i = 1,2,3$ for the change of mass relative to the previous three movements. To describe asymmetric responses to a rise and a drop of mass, the regressors $Rise_i$ and $Drop_i$ are used. If these asymmetric regressors were significant, their relevance was tested as follows: The symmetric regressor DM_i was forced into the equation. Only if the asymmetric regressor remained significant was it assumed to be relevant and only then was it presented. Besides these mass related regressors, some other regressors were used: the movement direction (dir), the movement number (trend), and per subject a parameter, which for this subject equals one and which is zero for other subjects. These regressors served mainly to reduce the variance and thus enhance the significance of the mass regressors. For reasons of brevity the parameters for subject dependence will not be presented in detail. Regressors were entered step-

wise, starting with the most significant regressors, until a significance level of 1% was reached.

The parameters in Table 2 describe the EMG and the kinematic signals. However, this description is not detailed enough to reveal the latency and the nature of the first effects of feedback. These aspects will be studied from plots of average EMG traces. This averaging was performed after alignment in time to the onset of the EMG activity of agonists that showed a clearly detectable activity in all subjects. For anteflexion, the average onset of the deltoideus pars anterior and the pectoralis major pars clavicularis was used and for retroflexion the deltoideus pars posterior and the latissimus dorsi. Before plotting the averaged EMG traces have been low pass filtered (35 Hz).

RESULTS

The first disturbed movements arrived at the desired position within reasonable time, albeit with

TABLE 3. Regressors

dir	movement direction, 1 = anteflexion (forward), -1 = retroflexion	
M	$M(n)$ the current mass, 0 = low, 1 = high mass	
DM_i	$M(n) - M(n - i)$, mass change	with $i = 1,2,3$
Drop _i	$MAX(-DM_i, 0)$	with $i = 1,2,3$
Rise _i	$Rise_i = MAX(DM_i, 0)$	with $i = 1,2,3$

n = movement number.

a movement trajectory different from previous movements (Figure 1). The EMG records showed considerable modifications of muscular activity, which were most apparent in the antagonist activity.

Kinematic Parameters

In the linear regression it appeared that most kinematic parameters were significantly and relevantly affected by the mass to be displaced (Tables 4a, b). The coefficients for M indicate a persistent dependence on the mass. Thus these coefficients describe the final result of adaptation. In both fast and submaximally fast movements, a higher mass led to an increased duration of the different movement phases and to a subsequent reduction in velocity. The coefficients for DM_i , $Rise_i$ and $Drop_i$ indicate temporary effects after the change of mass. Thus these coefficients describe the adaptation dynamics. Most of the dynamic parameters in Table 4 concern the first and second movement after a change of mass. Only for the velocity of submaximally fast movements, does adaptation seem to extend to the third movement. For a number of parameters, the regressors $Rise_i$ and/or $Drop_i$ are significant (Table 4). This demonstrates a difference in the temporal course of the adaptation process after a rise of mass and a drop of mass.

The response of the peak velocity V_{max} to a change of mass is depicted in Figure 2. Here it can be seen that V_{max} does not fully return to the original value. This is not surprising for maximally fast movements where limits on input amplitudes probably limit movement velocity. However, in the experiment at submaximal velocity, a velocity independent of the mass could have been obtained. Thus no support is found for the hypothesis that adaptation pursues a certain desired peak velocity. The last five parameters in Table 4 describe the shape of the movement trajectory after scaling to the movement velocity. For these dimensionless parameters, adaptation yields static values independent of the mass to displace. This follows from the fact that none of these parameters depends significantly on the regressor M (current mass). Thus it can be concluded that the adaptation process contributes to an invariant shape rather than to an invariant movement velocity. Several parameters deviate significantly for certain subjects. Among these are scaled parameters which indicate subject dependent movement trajectories. A number of

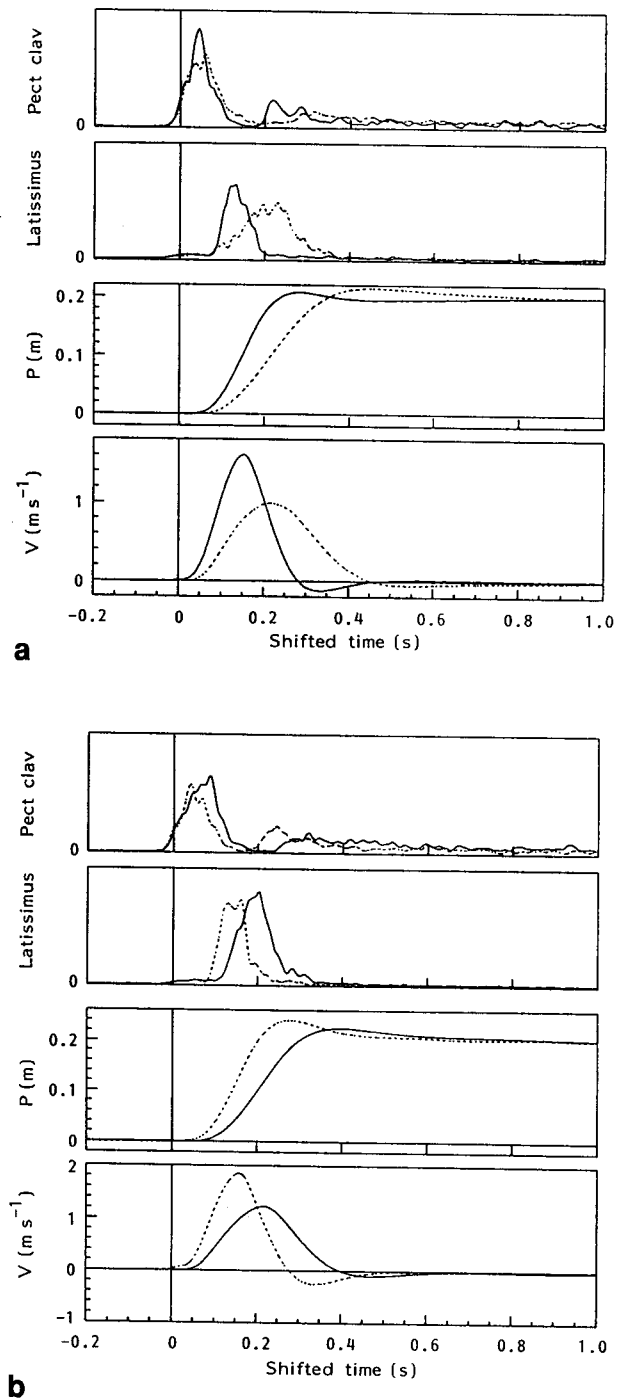


FIG. 1. Maximally fast anteflexion movements with a stationary mass (—) and first movements after a change of mass (---); **a**, mass rise from 0.6 to 5.6 kg; **b**, mass drop from 5.6 to 0.6 kg; traces contain from top to bottom: agonist EMG activity (pectoralis major pars clavicularis), antagonist EMG activity (latissimus dorsi), P = hand position, V = hand velocity; traces are averaged over movements from one subject after alignment in time towards the onset of agonist EMG bursts.

TABLE 4a. Submaximally fast movements, regression coefficients of dynamic response of kinematic parameters to mass change

Parameter	Regression coefficients*
V_{max} [ms^{-1}]	$0.913 - 0.127M - 0.028DM_1 - 0.033DM_2 + 0.025DM_3 + 0.023dir$
T_{dk} [ms]	$337 + 25Drop_1$
T_{ak} [ms]	$149 + 29M + 37Rise_1 + 25Rise_2$
T_{bk} [ms]	$214 + 54M - 6dir$
T_1 [ms]	150
R_c	0.29
T_{ak}/T_{bk}	$0.77 + 0.16Rise_1 + 0.08Drop_1$
T_{aks}	$153 + 26Rise_1$
T_{bks}	213
T_{1s}	$133 + 19dir$

Parameters defined in Table 2, regressors in Table 3. *Significant with $P < 0.01$ for t-test with separate variance analysis.

TABLE 4b. Maximally fast movements

V_{max} [ms^{-1}]	$1.590 - 0.373M - 0.201Rise_1 + 0.098Drop_1 + 0.042dir - 0.070DM_2$
T_{dk} [ms]	$315 + 37Drop_1$
T_{ak} [ms]	$104 + 29M + 4dir$
T_{bk} [ms]	$152 + 52M + 9DM_2 - 14dir$
T_1 [ms]	$91 + 68Rise_2$
R_c	$0.33 + 0.05dir$
T_{ak}/T_{bk}	$0.73 - 0.05DM_2 + 0.08dir$
T_{aks}	$161 - 14DM_2 + 10dir$
T_{bks}	$236 - 6DM_1 - 12dir$
T_{1s}	$140 + 27dir$

Further as in Table 4a.

parameters depends significantly on the movement direction dir (Table 4). In no parameter a significant trend was found in the current experiments.

These results for an unexpectedly varying mass were compared with parameters from experiments with a constant mass. This comparison was only made for the well defined task of maximally fast movements. The static behaviour following from Table 4b was in close accordance with parameters estimated for movements made with a constant mass. However, for a constant low mass, the ratio T_{ak}/T_{bk} was 0.77 and for a high mass this ratio was 0.68 ($P < 0.007$). Similar values were found in the experiment with varying mass but there the difference was not significant. The ratio T_{ak}/T_{bk} is dimensionless and thus must be constant when the shape is invariant. The significant difference in the constant mass experiment therefore contradicts the shape invariance indicated by the experiment with varying mass. Still this difference is rather small compared to the effects of mass on movement velocity and duration.

EMG Parameters

From the EMG records, timing and amplitude parameters were computed for 12 muscles. These parameters have been analysed, except for those of the trapezius and the deltoideus pars media in which no consistent pattern was observed in the subjects studied now.

The EMG regression parameters will not be presented in detail. The EMG timing parameters T_d , T_a , T_b showed qualitatively the same behaviour as respectively the parameters T_{dk} , T_{ak} , T_{bk} in Table 4 (which were estimated from movement kinematics). Agonist and antagonist burst durations T_a , T_b increased with a higher mass. The static dependence of nearly all EMG timing parameters on the mass was significant but the dynamic regressors DM_i , $Rise_i$, $Drop_i$ mostly did not meet the 1% significance level.

As could be expected, EMG amplitudes were strongly affected by the instruction regarding movement velocity. Compared to fast movements, in

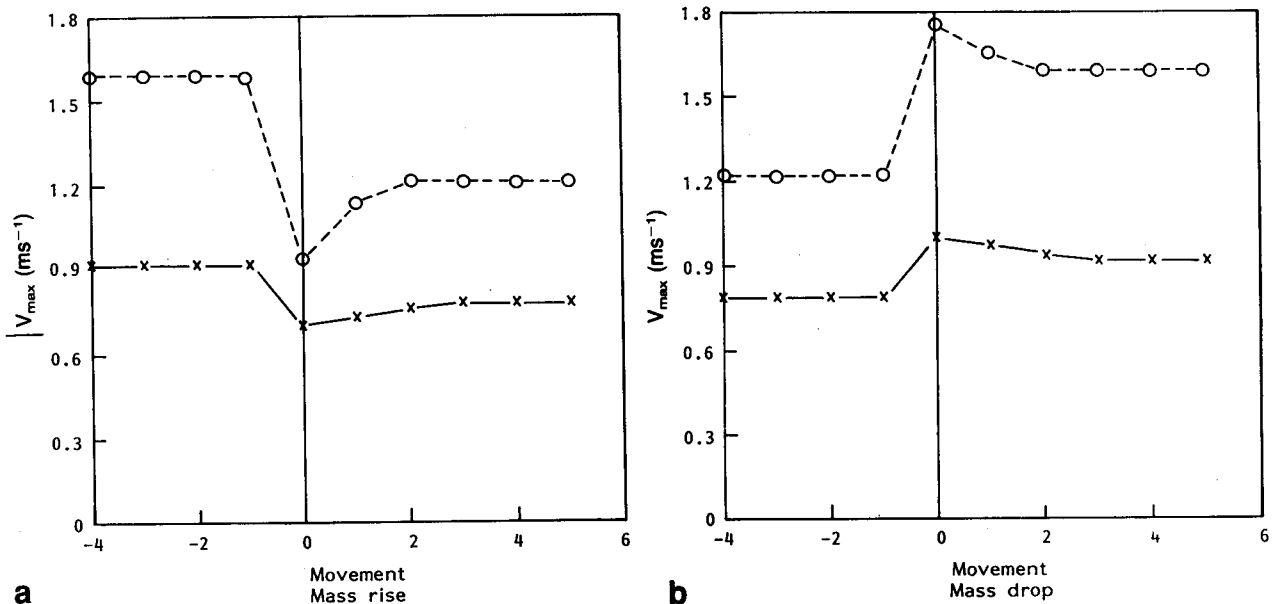


FIG. 2. Response of the peak velocity V_{max} to a change of mass, a, mass rise from 0.6 to 5.6 kg; b, mass drop from 5.6 to 0.6 kg; the movement number 0 is the first movement with a new mass; number 1 is the second movement with a new mass etc.; the response is based on the regression parameters from Table 4; the two lines describe maximally fast and submaximally fast movements respectively.

submaximally fast movements agonist amplitudes were about 40% and antagonist amplitudes were about 50%. The mass variations had far smaller effects on EMG amplitudes; effects on the agonist amplitudes were very small and insignificant for all prime movers.

Plot of EMG and Kinematic Signals

From the parametric analysis of the EMG records, a variation of timing rather than amplitude emerged. However, these parameters describe durations of about 60–150 ms and average amplitudes over these durations. A more detailed analysis of the first phase of the EMG activity will be given now to assess the first effects of the mass variations.

Figure 3 describes the activity of two agonist and two antagonist muscles for a high mass, just after a drop of mass and for a low mass. Thus Figure 3 shows movements before the disturbance, just after the disturbance and after adaptation. It can be seen that, after a drop of mass, activity is first similar to the undisturbed activity. Between $t = 30$ and 70 ms, agonist activity is increased ($P < 0.007$ for two-sided t -test). After $t = 70$ ms, agonist activity is reduced ($P < 0.001$) and after 80 ms antagonist activity is increased. After a drop of mass, displacement and velocity will be greater than expected.

Thus feedback of displacement and/or velocity would naturally lead to a reduction of agonist inputs and/or an increase of antagonist inputs. This explains the later reduction of agonist activity and increase of antagonist activity. However, the early increase of agonist activity is quite unexpected. Unfortunately this finding is not fully consistent over the various muscles and subjects: The unexpected increase was found mainly during maximally fast movements but not in the fastest movement. In the other three subjects it was found in nine out of 21 cases. Here each case represents one muscle in one subject. Furthermore, only the serratus anterior, deltoideus pars anterior and posterior, latissimus dorsi and the parts of the pectoralis major were considered as only these muscles clearly acted as agonists in either forward or backward movements.

After a rise of mass a similar reaction was found; first a reduction of agonist activity and later, an increase of agonist activity and a reduction or delay of antagonist activity. Again, the first reaction is unexpected and the second reaction is expected. Such an unexpected reduction of agonist activity was found mainly during maximally fast movements where it occurred in 17 out of the 28 cases formed by the four subjects and the muscles just mentioned. The effect was observed in all four subjects in the two parts of the pectoralis.

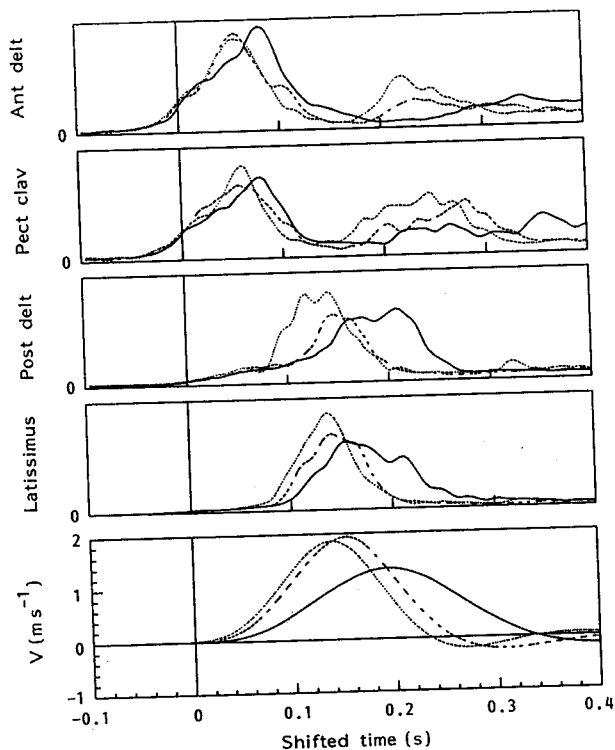


FIG. 3. Mass drop in maximally fast anteflexion movements; traces contain from top to bottom: agonist EMG activity of the deltoideus pars anterior and the pectoralis major pars clavicularis, the EMG activity of the deltoideus pars posterior and the latissimus muscle. The unexpected modifications of agonist activity are found as little as 25 ms after movement onset. While these early feedback effects are unexpected and not fully consistent, on average about 90 ms after movement onset, effective and substantial modifications of muscular activity appear that are largely consistent over subjects and muscles.

DISCUSSION

At the onset of goal-directed movements the inertial load to be displaced was changed unexpectedly. The first disturbed movements arrived at the desired position within reasonable time, albeit with a movement trajectory different from that of previous movements (Figure 1). Significant differences were found between the first two or three

movements after a change of mass (Table 4, Figure 2). These differences prove that adaptation takes place. This can be argued as follows. The mass is changed at the onset of certain movements. Then the dynamics of the arm plus load remain constant during several following movements. The fact that movement parameters change during these movements must therefore be caused by an adaptation of the control strategy.

It can be argued that the successful completion of the first disturbed movement is mainly due to feedback. This implies relatively fast feedback combined with slower adaptation which is common in control theory. Such an adaptation could even be a discrete process in which information from one movement is used to adapt the control strategy for following movements as suggested in Ottenhoff²¹. However, alternatively, adaptation may already be effective within the first disturbed movement. An argument for such a fast adaptation is given in Smeets et al.²⁶ where it was concluded that modifications of muscular activity in the first movements with a changed mass could not be explained by linear position or velocity feedback. It is concluded that there is a more complex use of sensory information already in the first disturbed movement²⁶. This is called reprogramming which falls well within our definition of adaptation.

Significant adaptation effects were demonstrated in the first two or three movements after a change in the load. Similar experiments studying adaptation over six movements do not indicate significant adaptation after the third movement (unpublished results).

As to the nature of the adaptation process, we have the following observations: Subjects can increase movement impedance by co-activation of antagonist muscles and by increasing of feedback gains. This is a well documented adaptation mechanism to uncertain conditions^{16,30,33}. Yet in our experiment co-activation is negligible. We therefore consider the following aspects to be possibly adapted:

1. a load parameter; the mass;
2. closed-loop controls (feedback gains);
3. open-loop controls (motor programs).

Of course, adaptation of a load parameter is only

useful if serving to adapt closed-loop or open-loop controls. Adaptation of a load parameter is the most powerful option: with one parameter the control of all degrees of freedom in the arm can be adapted. Using the 'knowledge' that only the load changes, only this global parameter has to be estimated in some way, which can be done in a relatively short time. The controls can be adjusted by using knowledge of how the system can be controlled given a certain mass. This knowledge may be the result of a much longer learning process. Such an adaptation of the control strategy based on adapted load parameters is a process which requires an internal representation of some kind.

Alternatively, adaptation can affect closed-loop or open-loop controls directly. Direct adaptation of feedback gains could be performed by modification of the gains of all muscles in a similar fashion, for instance multiplying all gains with the same factor. Yet, such a simple adaptation is presumably sub-optimal. Optimal adaptation of closed-loop and/or open-loop terms will be more complex as controls for several muscles will have to be adapted. It may be doubted whether such an adaptation could be completed in only a few movements.

The experiment contained both forward and backward movements. Thus information is provided on in how far adaptation for these directions is a separate process. Finding a separate process would indicate that direction-specific information like a motor program is adapted. In case of a separate process, information from a first disturbed movement would not be used to adapt the second movement which has an opposite direction. Thus behaviour would only depend on the current mass M and the mass two movements ago $M(i-2)$ and possibly four movements ago etc. In the regression (Table 4) such behaviour would lead to dominance of the parameters DM_2 , $Rise_2$ and $Drop_2$ and absence of DM_1 , $Rise_1$, $Drop_1$ and DM_3 , $Rise_3$ and $Drop_3$. Table 4 and Figure 2 do not show such a dominance, instead a rather continuous adaptation is observed. This indicates a combined adaptation for forward/backward movements.

With regard to the goals of adaptation, assuming that adaptation is successful and that the movements obtained reflect the goals of the adaptation, we have the following observations. We found that after adaptation, the movement velocity still strongly depended on the mass. So, adaptation does not retain the old trajectory. After scaling towards velocity, a shape invariance was demonstrated. Thus

it can be concluded that the adaptation process contributes to an invariant shape rather than to an invariant movement velocity. Apparently the desired movement velocity is adapted to the load. Here it must be noted that in the experiment with constant low or high mass a slight but significant deviation from the shape invariance was demonstrated. These results largely support Ruitenbeek²³ who concluded on a shape-invariance in various conditions in relatively slow movements. We found the shape to be practically independent of mass. In fast movements however, the shape does depend strongly on the movement direction (Table 4b and Happee¹³).

The EMG records reflect muscular activity which results from neural inputs. EMG timing was strongly affected both by the instruction regarding movement velocity and by the mass variations. EMG amplitudes strongly depended on the instruction regarding movement velocity. Gottlieb et al.⁶ relate EMG amplitudes (and acceleration) to instructions regarding movement velocity and not to the desired displacement. Such task dependent input levels may actually be determined by the size of the recruited motoneuron populations. Pre-determined input levels would largely constrain the effect of adaptation. Trajectories after adaptation may follow from these constraints rather than from goals like a shape-invariance. As stated in the introduction such pre-determined input levels were not expected in submaximally fast movements.

In the first movements after a change of mass, effective and substantial modifications of muscular activity appear about 90 ms after movement onset. Subtracting a delay between EMG onset and detectable movement of about 20 ms, this indicates feedback latencies below 70 ms. This latency allows relatively complex processing by multi-synaptic pathways. Thus adaptation within the agonist burst of the first movement seems possible.

One would expect that with an increased mass, feedback increases agonist activity to obtain the desired displacement. With a decreased mass a decrease in agonist activity would be expected. Such effects would follow naturally from a position (and velocity) feedback using for instance, information from the muscle spindles. (At least when assuming negative closed-loop gains as is required for stabilizing feedback of position and velocity). Such feedback effects are found in numerous disturbance experiments and are commonly referred to as the stretch reflex. However, in the literature opposite effects are also found in some conditions and mentioned

as the shortening reflex¹. The first and unexpected effect of feedback (Figure 3) could be due to such a shortening reflex. The neurological origin of such reflexes is obscure¹. Shortening reflexes can theoretically be explained by a velocity or acceleration feedback with positive closed-loop gain²⁵. A feedback component with a positive closed-loop gain will have a de-stabilizing effect, however in combination with other feedback components with a negative feedback gain stability can be obtained. A more reasonable explanation is the presence of force feedback with a negative gain. After a decreased mass, the resisting force in the hand will be lower than expected. This will lead to increased acceleration and velocity. Due to the force-velocity relation this will lead to reduced muscle forces. Negative feedback of either the force on the hand or the muscle force could thus explain our findings. In particular the force on the hand is strongly and early affected by the load. This would also explain the early occurrence of this feedback component. Yet, it must be noted that this finding is not fully consistent over the various subjects and muscles.

Such a force feedback does not seem to be useful. However, it would help stabilizing the system as has been verified in a simulation study. A model was used with one degree of freedom, two muscles (non-linear, third-order) with a sensory delay of 50 ms. For this model feedback was optimized assuming feedback of muscle length and velocity. Adding feedback of muscle force allowed increased position and velocity feedback gains. Thus adding force feedback yielded a doubling of system bandwidth¹⁵. Force feedback will also affect the response to mechanical perturbations; while position feedback records of prime movers, muscles acting on the scapula, one rotator cuff muscle, and a shoulder-elbow muscle. In reaction to force pulses, in Happee¹⁴ similar reactions were also found in all shoulder muscles. These results indicate a tight coupling of the control of these shoulder muscles. However, the analysis of these effects is complicated by the large variations between subjects in the normal (undisturbed) function of in particular the trapezius and the infraspinatus. It seems important to gain understanding in these variations. Possible

explanations may lie in the way the subjects held their shoulder, or in measurement problems related to electrode placement.

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