

RESEARCH ARTICLE

M. Ioffe · J. Massion · N. Gantchev · M. Dufosse
M.A. Kulikov

Coordination between posture and movement in a bimanual load-lifting task: is there a transfer?

Received: 26 August 1994 / Accepted: 11 December 1995

Abstract The present experimental series was designed to test the possibility that an anticipatory postural adjustment learned during the performance of a bimanual load lifting task may be transferred between the upper extremities. Eight seated subjects were asked to maintain horizontally one forearm (postural arm) loaded with a 1-kg load, which was fixed to the arm by means of an electromagnet. The unloading was triggered either by the experimenter pressing a switch (control) or by the subjects making a voluntary movement with their other arm (moving arm). In the latter case, the subject lifted a 1-kg load resting on a force platform with the moving hand, and the switching off was triggered when the force level reached a threshold of 0.5 kg. The maximum amplitude (MA) and the maximum velocity (MV) of the postural forearm elbow joint rotation occurring after the unloading were measured at each trial. The learning process was estimated by performing a regression analysis on each series of trials, using an exponential model, and from the intercept of the regression curve with the ordinate. 1. During the original learning session (three series of 20 trials), a decrease in MA and MV was found to occur both within the series and between the series during a session. 2. After the initial learning session, the sides of the postural and moving arm were interchanged to test whether any transfer had occurred. The first series of trials in the second session (transfer) and the last series of trials in the original learning session were compared and found to be significantly different in terms of the intercept (seven subjects in the case of MA, five subjects in the case of MV) and the slope (five subjects), indicating a lack of transfer. 3. The data recorded during the second transfer learning session indicated that learning occurred in all eight subjects in the case of MA and in six subjects

in the case of MV. It was observed that the original learning session did not facilitate the second one. 4. The lack of transfer of the anticipatory postural adjustment observed in this task is discussed with reference to the data in the literature.

Key words Posture · Movement · Bimanual coordination · Motor learning · Learning transfer · Human

Introduction

Manipulating heavy objects is a task commonly performed in everyday life. When a load supported by one hand is lifted off by the other hand, the position of the “postural” forearm remains unchanged, although the disturbance resulting from the unloading might be expected to trigger an upward forearm movement for mechanical reasons. This lack of forearm movement is due to an “anticipatory” postural adjustment associated with the lifting movement, consisting of an inhibition of the postural forearm flexors which starts before the onset of unloading (Hugon et al. 1982; Dufossé et al. 1985). This anticipatory postural adjustment minimizes the forearm position disturbance induced by the voluntary movement. It is one example of the more general class of anticipatory postural adjustments associated with voluntary movements, which are learned together with the movement and serve to prevent disequilibrium or the disturbance of the position of particular segments (head, trunk, arm, etc.) resulting from the performance of the movement (see Massion 1992).

One of the advantages of the bimanual load-lifting task in studies of this kind is that, unlike the other existing examples of posturokinetic coordination, where the anticipatory postural adjustment mainly involves the axial musculature, the postural task is specific to one forearm and the voluntary movement to the other. It was thus possible to evaluate the deficits due to unilateral brain lesion both as a function of the localization of the lesion and depending on

M. Ioffe · M.A. Kulikov
Institute of Higher Nervous Activity and Neurophysiology,
Academy of Sciences, Butlerova 5A, Moscow, Russia

J. Massion (✉) · N. Gantchev · M. Dufosse
Laboratory of Neurobiology and Movements, CNRS, 31,
chemin Joseph Aiguier, F-13402 Marseille Cedex 20, France;
Fax: +33-91775084

the tasks performed by each arm. Interestingly, these anticipatory postural adjustments are still present after corpus callosum section. They therefore belong to the category of long-learned bimanual tasks that split-brain patients are still able to perform (see Geffen et al. 1994). Anticipatory postural adjustments, moreover, were previously said to be impaired after lesion of the supplementary motor area (SMA) region and the motor cortex, when the contralateral arm was the postural forearm and not when it was the moving arm (Viallet et al. 1992). It has been proposed that the adaptive postural networks responsible for the anticipatory postural adjustments of the postural forearm may be located at some subcortical level and activated by collaterals of the corticospinal pathways arising from the cortex contralateral to the lifting movement. The specific role of the SMA area contralateral to the postural forearm might consist of selecting the appropriate postural reference frame for the task, i.e., of choosing the position of the postural forearm and gating the learned postural networks which minimize the postural disturbance due to the performance of the voluntary movement.

The learning of this posturokinetic coordination has been investigated by several authors (Paulignan et al. 1989; Forget and Lamarre 1990). The stabilization of the postural forearm can be acquired, for example, when a movement performed by one forearm artificially triggers the unloading of the postural forearm. The coordination can be acquired when elbow flexion is replaced by elbow extension. This is also the case when the voluntary movement triggering the unloading is a leg movement. Interestingly, learning occurs only in the presence of sensory afferents (Forget and Lamarre 1990).

As very little information is available about the learning of the anticipatory postural adjustments associated with voluntary movements, the main purpose of the present investigation was to answer the following question: is the anticipatory postural adjustment learned with the postural forearm on one side transferred to the other side after the sides of the postural and moving arms have been interchanged? Our hypothesis was that the coordinated task, including both the movement itself and its specific anticipatory postural adjustment, may be transferred as a whole, as are unimanual learned motor skills (Parlow and Kinsbourne 1989, 1990; Cohen et al. 1990; Parlow and Dewey 1991). Using the same learning procedure as Paulignan et al. (1989), where the load release was triggered by the other arm's load lifting movement, we concluded that no transfer occurred after the postural arm and the moving arm had been interchanged.

Materials and methods

In this experimental version of the bimanual load-lifting task, one forearm (the postural forearm) was kept in a given position, whereas the other arm (the moving arm) lifted a load. Four right-handed and four left-handed subjects were tested in the present study. Two learning sessions were run with each subject. At the first session, either the non-dominant arm (one right-handed, two left-handed) or the dominant arm (three right-handed, two left-handed) was tested first as the postural arm.

Experimental setup

The subjects were seated on a hard-backed chair, equipped with a support to which the arm could be fixed vertically just above the elbow. They were instructed to gaze horizontally at a line on the wall of the room 4 m in front of them, and to maintain the postural forearm horizontally, semiprone during the whole session. This forearm carried a platform equipped with strain gauges, from which a 1-kg load was suspended by means of an electromagnet. The unloading could be triggered in one of two ways: (1) the load was released by the experimenter switching off the electromagnet at unpredictable times (control situation); or (2) the load was released by the subject lifting a weight from a force platform with the other arm (learning situation).

During the learning session, the subject was asked to place the fingers of the moving arm around the weight before starting the movement and to lift the 1-kg load to about 10 cm above the steady platform equipped with strain gauges as fast as possible in response to a tone signal. The decrease in the weight to half of its initial value was the signal which triggered the load release on the side of the postural arm.

The general procedure at each learning session was as follows: first a series of 20 control load releases, then two series of 20 load releases triggered by the other hand-lifting movement; a second control series of 10–15 trials; a third series of 20 load releases triggered by the other hand-lifting movement. Occasionally, one or a few additional trials were performed in some series.

Once the first (original) training session had been completed, a second (transfer) session was performed with the other forearm acting as the postural arm. The duration of the whole experiment was about 2 h. A 5-min rest period was allowed after each series of trials in order to prevent fatigue.

Parameters recorded

The parameters recorded were the left and right forearm positions, which were monitored by means of potentiometers placed along the elbow joint axis, and the force recorded by the strain gauges on the platforms supporting the weight on each side. The electromyographic (EMG) activity of the brachioradialis on each arm was recorded using bipolar surface electrodes. An accelerometer placed at the level of the wrist on the postural forearm was used to monitor the vertical acceleration (Fig. 1). The analog parameters were digitized and stored on a computer disk (sampling rate 1000 Hz) for analysis.

Data analysis

Any changes in the postural forearm position after unloading were quantified by means of two indexes: the maximum amplitude (MA) and the maximum velocity (MV) of the upward movement of the postural forearm after unloading. Both indexes were computed within 600 ms of the perturbation onset. In fact, the MA was usually reached between 250 and 300 ms and the MV occurred within 100 ms of the onset of unloading. As the interval between the onset of unloading and the mechanical changes resulting from a spinal reflex action is around 100 ms (see Paulignan et al. 1989), any decrease in the MV was taken to reflect changes in joint stiffness prior to the onset of the perturbation onset (anticipatory postural adjustment). A decrease in the MA could result either from an anticipatory postural adjustment, when the MV also decreased, or from the action of the unloading reflex (Angel et al. 1965; Paulignan et al. 1989).

Statistical analysis

The data were analyzed with the STATGRAPHICS software program. Regression analysis was carried out to determine the changes in the MA and MV of the unloading during repeated trials. An exponential model was used to approximate the experimental curves. The slope of the regression curves and the intercept of the regression curve with the ordinate were used to estimate the intensity of

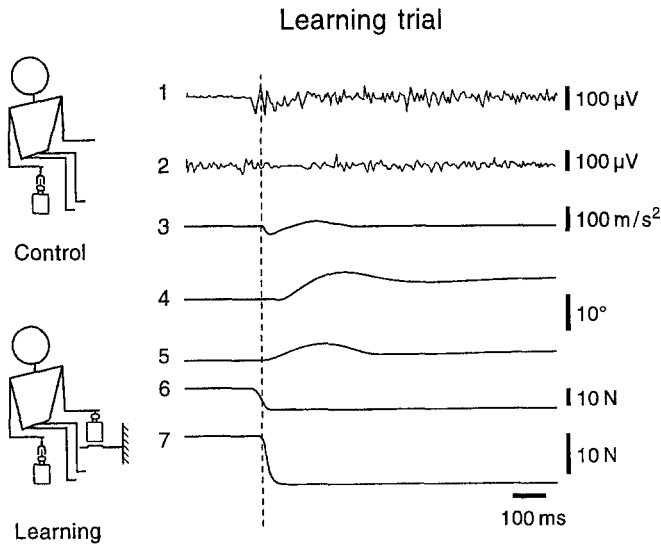


Fig. 1 Parameters recorded. On the *left*, diagram of the control conditions (the unloading was triggered by the experimenter) and the learning situation. On the *right*, recordings from a single trial during a learning series. 1 and 2: EMG from the brachioradialis of the lifting (1) and postural (2) arms. Note in 2 the unloading reflex. 3: accelerometric trace recorded on the wrist of the postural arm. 4 and 5: elbow angle of the lifting (4) and postural arm (5). 6 and 7: force platform recording on the side of the lifting (6) and supporting (7) arms. The striped vertical line indicates the onset of the unloading of the postural forearm

learning within and between series. The regression curves with each subject and the level of intercept were compared using Student's *t*-test ($P < 0.05$). This analysis seemed to be an appropriate means of estimating the significance of the differences between series during learning and transfer sessions for the following reasons.

The least-squares method shows that, in the majority of series, the changes in MA or MV were well approximated by an exponential model, where the logarithm of the amplitude was a linear function of the rank number of the trial:

$$y = a + bx + e \quad (1)$$

where y is the logarithm of the MA, a and b are the coefficients giving the point of intercept of the line with the axis of MA (a) and the slope of the line with respect to the axis of trial numbers (b), x is the rank number of the trial, and e is the deviation of experimental values from the calculated ones (calculations of a and b variables for the regression equation and for exponential smoothing curve are made by the same least-squares method, and give the same values). We assume in our analysis that, in the process of learning, the decrease in MA is proportional to the MA value and that the coefficient of this proportionality remains constant during the learning process. The deviations from the expected value of this coefficient are determined by factors which are not controllable during the experiment; they do not depend on the rank number of the trial and are proportional to the amplitude.

These assumptions allowed us to use the first model of regression analysis, which is described by equation (1), where y is the response variable, e is the deviation of y from the value $a + bx$ (y and e are assumed to be random values), a and b are unknown values which are estimated by the use of the least-squares method, and x is the controlled variable (the rank number of the trial).

We make the following assumptions about the errors e :

1. e are not biased.
2. e are not correlated among the various trials.
3. e distribution has the same variances for different x (homoscedasticity).
4. e are approximately normally distributed.

Checking assumption 4 showed that this does not contradict the experimental data. Assumption 3 cannot be tested without the repetition of learning. It has been established, however (Seber 1977), that a moderate violation of these assumptions does not lead to serious errors.

Proceeding from the validity of the assumptions mentioned above, we can consider the intercept and slope of the regression curves as statistical values and compare these values between different series. In this case, the assumption about the independence of the estimations in two different series seems to be valid, because it is impossible to establish the correspondence between amplitudes of the trials with the same rank numbers in different series.

A two-factor ANOVA was also performed to analyze the effects of the motor dominance and the learning sequence (whether the dominant or nondominant arm was used first in the training sessions) on the results obtained.

Results

Control series

Unloading triggered by experimenter

In the control series, the unloading was triggered by the experimenter switching off the electromagnet. As described previously (Paulignan et al. 1989), this was followed by an upward forearm movement, which reached a

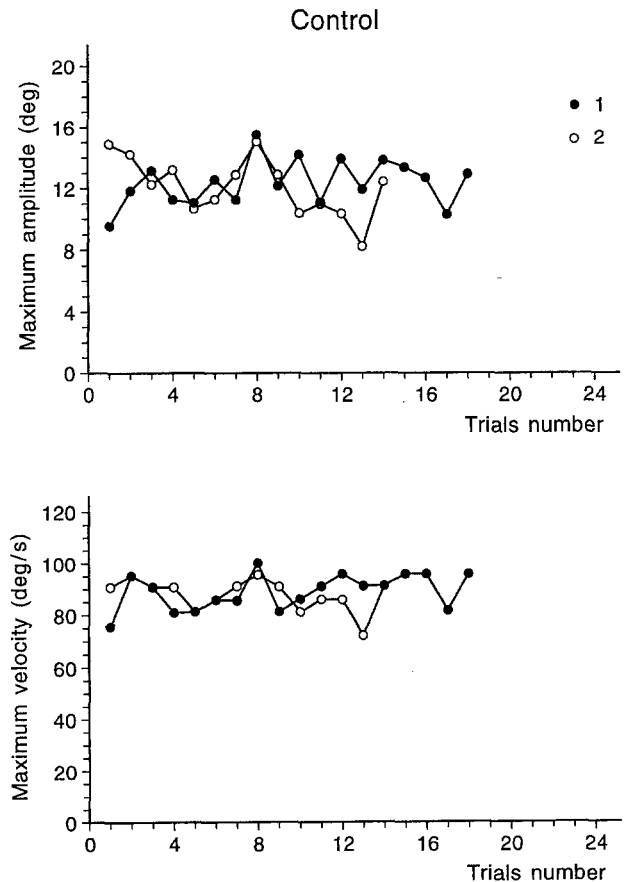


Fig. 2 Control series in one subject. Maximum amplitude and velocity of the elbow angle after forearm unloading. Maximum amplitude and maximum velocity in two control series (1, 2). On the ordinate, elbow angle in degrees or elbow angle velocity in degrees per second. On the abscissa, the successive trials in the series

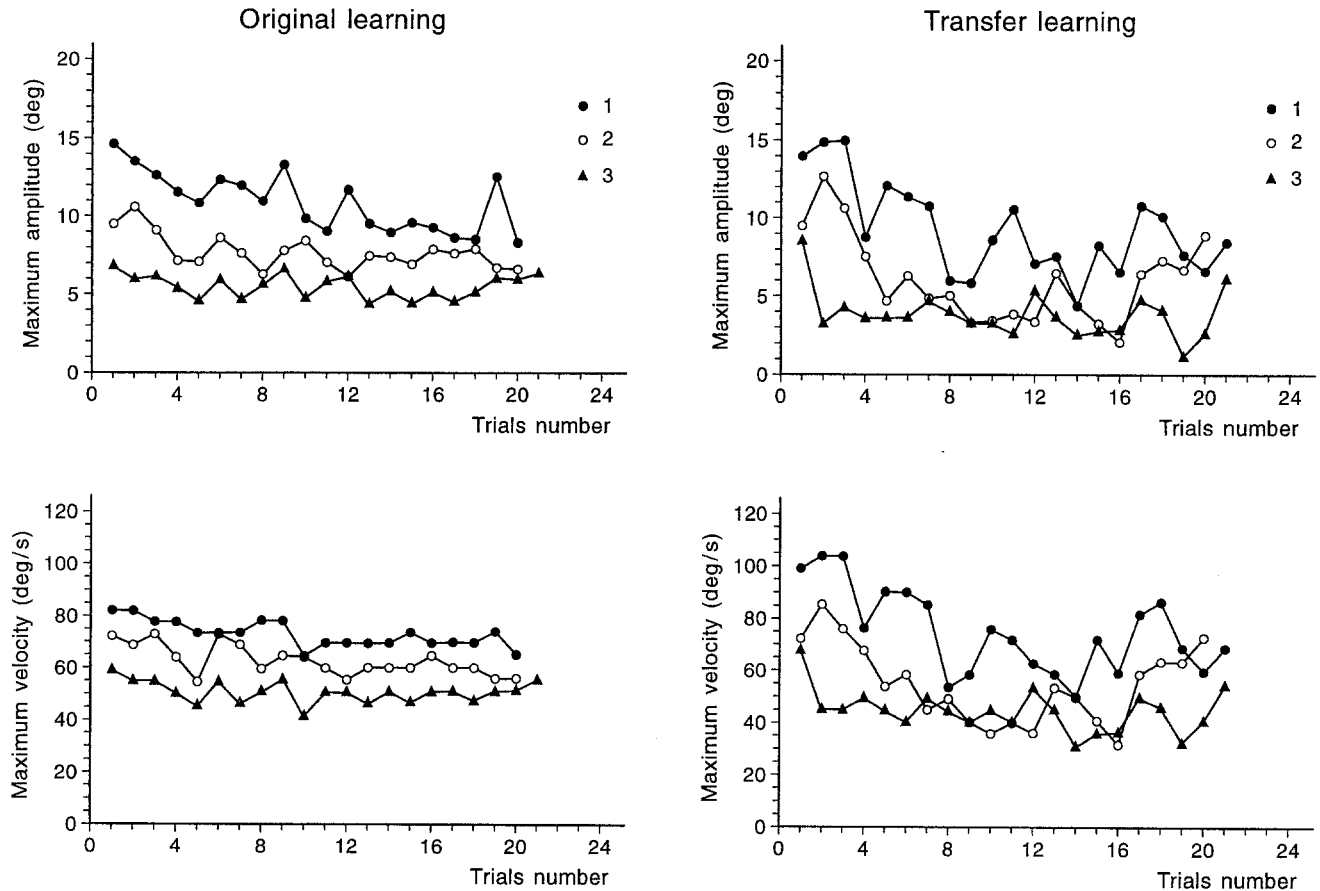


Fig. 3 Original learning session (*left*). Maximum amplitude (MA) and maximum velocity (MV) after right limb unloading triggered by the lifting movement of the left arm in three successive series (1, 2, 3). Transfer learning session (*right*). MA and MV after left limb unloading triggered by the lifting movement of the right arm in three successive series

maximum after some 250 ms and then decreased to a stable value at about 400 ms, without any marked oscillations. The final position was higher than the initial position. Figure 2 shows the MA and the MV in successive individual trials in the control series. The mean control MA in the various subjects ranged from around 5 to 12° and the mean control MV from around 40 to 108°/s. Looking at successive trials, one can see that the MA and MV fluctuated somewhat from one trial to another, but they showed no very marked tendency to decrease in the course of a series. This was supported by the results of the regression analysis: the slopes of the corresponding regression curves were not significantly different.

Learning during repeated series of unloading triggered by the subject (original learning session)

At the first experimental session, we studied the changes in the MA and MV of the postural forearm's upward movement when the unloading was triggered by the subject lifting a weight with the other hand. This procedure was used in a previous study by Paulignan et al. (1989), where the MA and MV of the forearm's upward shift de-

creased during the repeated trials. In the present study, we compared individual regression curves to establish whether this decrease was significant. The intercepts of the regression curves with the ordinate gave the level of MA and MV at the onset of a series, and this served as an index to the learning in comparison with the control level. The slope of the regression curves was analyzed with a view to estimating and comparing the intensity of the decrease. Figure 3 shows the changes in the MA and MV in three successive series in one of the subjects. By comparing Figs. 2 and 3, one can see that the initial MA and MV values in the first series were close to the control level, but that the MA and MV gradually decreased during the series. The MA and MV of the postural forearm's upward shift after the unloading also decreased during the successive series. The difference between the intercepts of the regression curves in the first and the third series was significant in all the subjects as regards both the MA and MV (Table 1, L1/L3; R1/R3; first limb). Learning can therefore be said to have occurred both during a single series and from one series to another.

Testing for transfer

After the 3 learning series at the first original learning session, the subjects were tested for transfer: the postural and moving arm were interchanged. Figure 3 illustrates the results of this testing session. A great difference can be seen to have existed between the results of the last se-

Table 1 Intercept differences between the exponential regression curves giving the maximum amplitude and the maximal velocity of elbow rotation in each experimental series (*t*-test). Evaluation of the learning processes during successive series of unloading on the left and right sides, respectively, and the evaluation of the transfer. (*L1*, *L2*, *L3* first, second, and third learning series, with the left forearm acting as the postural arm, *R1*, *R2*, *R3* first, second, and third learning series, with the right forearm acting as the postural arm, / the *t*-test comparisons between two series) * *t*<0.05; ** *t*<0.01; *** *t*<0.001

	Left side, L1/L3	Right side, R1/R3	Transfer		
			R3/L1, L3/R1	R1/L1	R3/L3
Intercept amplitude					
F.M.	<i>t</i> =7.8*** 1st limb	<i>t</i> =2.69* 2nd limb	<i>t</i> =8.46***	<i>t</i> =0.003	<i>t</i> =6.6***
H.M.	<i>t</i> =4.47 2nd limb	<i>t</i> =9.78** 1st limb	<i>t</i> =5.28***	<i>t</i> =0.8	<i>t</i> =1.08
E.M.	<i>t</i> =5.98*** 1st limb	<i>t</i> =5.74** 2nd limb	<i>t</i> =6.8***	<i>t</i> =2.23*	<i>t</i> =0.46
Y.S.	<i>t</i> =3.23** 2nd limb	<i>t</i> =4.6*** 1st limb	<i>t</i> =1.17	<i>t</i> =1.89	<i>t</i> =2.9**
L.M.	<i>t</i> =6.68*** 2nd limb	<i>t</i> =9.51*** 1st limb	<i>t</i> =7.53***	<i>t</i> =3.61***	<i>t</i> =2.9**
L.L.	<i>t</i> =2.26* 1st limb	<i>t</i> =4.16*** 2nd limb	<i>t</i> =2.18*	<i>t</i> =0.05	<i>t</i> =1.76
S.A.	<i>t</i> =2.45* 2nd limb	<i>t</i> =3.2** 1st limb	<i>t</i> =2.77*	<i>t</i> =1.03	<i>t</i> =1.27
P.B.	<i>t</i> =2.95** 2nd limb	<i>t</i> =4.92*** 1st limb	<i>t</i> =6.47***	<i>t</i> =0.79	<i>t</i> =4.35***
Intercept velocity					
F.M.	<i>t</i> =7.18*** 1st limb	<i>t</i> =3.84*** 2th limb	<i>t</i> =8.78***	<i>t</i> =0.49	<i>t</i> =4.79***
H.M.	<i>t</i> =5.36*** 2nd limb	<i>t</i> =9.27*** 1st limb	<i>t</i> =6.06***	<i>t</i> =1.58	<i>t</i> =0.58
E.M.	<i>t</i> =3.11** 1st limb	<i>t</i> =4.79*** 2nd limb	<i>t</i> =5.1***	<i>t</i> =0.44	<i>t</i> =0.51
Y.S.	<i>t</i> =3.28** 2nd limb	<i>t</i> =3.48*** 1st limb	<i>t</i> =0.06	<i>t</i> =2.48*	<i>t</i> =3.76***
L.M.	<i>t</i> =5.84*** 2nd limb	<i>t</i> =9.66*** 1st limb	<i>t</i> =7.15***	<i>t</i> =4.98***	<i>t</i> =2.4*
L.L.	<i>t</i> =2.02* 1st limb	<i>t</i> =3.52*** 2nd limb	<i>t</i> =0.74	<i>t</i> =1.24	<i>t</i> =2.73**
S.A.	<i>t</i> =0.41 2nd limb	<i>t</i> =2.74** 1st limb	<i>t</i> =1.25	<i>t</i> =3.34**	<i>t</i> =1.00
P.B.	<i>t</i> =0.43 2nd limb	<i>t</i> =4.47*** 1st limb	<i>t</i> =4.96***	<i>t</i> =0.41	<i>t</i> =5.09***

ries in the original learning session and the first series in the transfer learning session. In the first few trials run after changing the postural arm, the MA and MV were similar to the control values and decreased during the first series in the same way as in the first series of the original learning session. The regression analysis showed the existence of significant differences in the intercept between the last series of the original learning session and the first series of the transfer learning session in seven subjects as regards the MA and in five subjects (some of whom were the same as the latter and others different) as regards the MV (Table 1: transfer, L3/R1; R3/L1). On the basis of the intercept, these results therefore indicate that in the majority of the subjects no transfer occurred. The analysis of the slope was not so clear-cut, however, at least as far as the MA was concerned: a significant difference was found to exist between the last series of the original learning session and the first series of the second learning session in four subjects (Table 2: transfer, L3/R1; R3/L1). The slopes of the MV curves were significantly different in the five subjects who showed a significant difference as regards the intercept. (Table 2: transfer, L3/R1; R3/L1). The ANOVA test showed that the results did not depend on either the motor dominance of the subject ($F_{(1,4)}=1.02$; $P=0.37$) in the case of MA

and ($F_{(1,4)}=0.19$; $P=0.69$) in that of MV or on the sequence of learning ($F_{(1,4)}=0.001$; $P=0.98$) in the case of MA and ($F_{(1,4)}=0.057$; $P=0.82$) in that of MV (whether the initial learning involved the dominant limb or vice versa).

Learning after changing the side of the postural limb (transfer learning session)

Figure 3 shows the changes in the MA and the MV which occurred in three successive series after the side of the postural arm was changed. During these series, a gradual decrease in the MA and MV occurred. A significant difference was found to exist in the level of intercept between the regression curves recorded during the first and third series in this session in all eight subjects in the case of MA and in six subjects in that of MV (Tables 2: L1/L3, R1/R3, second limb). These data therefore suggest that a new learning process took place after the side of the postural arm had been changed.

Upon comparing the final level of this new learning process with the final level of the original learning session (R3/L3), significant differences were observed among four subjects as regards the MA and among five subjects as regards the MV. Among the subjects showing

Table 2 Slope differences between the exponential regression curves based on the maximum amplitude and maximum velocity of elbow rotation in each experimental series (*t*-test). See Table 1 for further explanation

	Left side, L1/L3	Right side, R1/R3	Transfer		
			R3/L1, L3/R1	R1/L1	R3/L3
Slope amplitude					
F.M.	<i>t</i> =3.22** 1st limb	<i>t</i> =0.39 2nd limb	<i>t</i> =3.89***	<i>t</i> =0.27	<i>t</i> =3.37***
H.M.	<i>t</i> =0.29 2nd limb	<i>t</i> =2.39* 1st limb	<i>t</i> =1.96	<i>t</i> =0.46	<i>t</i> =1.18
E.M.	<i>t</i> =2.66* 1st limb	<i>t</i> =2.68* 2nd limb	<i>t</i> =4.3***	<i>t</i> =2.06*	<i>t</i> =1.42
Y.S.	<i>t</i> =0.61 2nd limb	<i>t</i> =0.9 1st limb	<i>t</i> =0.19	<i>t</i> =0.81	<i>t</i> =0.94
L.M.	<i>t</i> =0.73 2nd limb	<i>t</i> =4.68** 1st limb	<i>t</i> =2.38*	<i>t</i> =3.88***	<i>t</i> =1.76
L.L.	<i>t</i> =0.32 1st limb	<i>t</i> =0.12 2nd limb	<i>t</i> =0.21	<i>t</i> =0.68	<i>t</i> =0.07
S.A.	<i>t</i> =0.72 2nd limb	<i>t</i> =0.68 1st limb	<i>t</i> =0.13	<i>t</i> =1.19	<i>t</i> =0.25
P.B.	<i>t</i> =1.19 2nd limb	<i>t</i> =3.75*** 1st limb	<i>t</i> =4.09***	<i>t</i> =0.19	<i>t</i> =0.21
Slope velocity					
F.M.	<i>t</i> =3.07** 1st limb	<i>t</i> =2.02* 2nd limb	<i>t</i> =4.98***	<i>t</i> =1.17	<i>t</i> =3.39**
H.M.	<i>t</i> =0.99 2nd limb	<i>t</i> =1.48 1st limb	<i>t</i> =2.22*	<i>t</i> =1.56	<i>t</i> =1.08
E.M.	<i>t</i> =0.04 1st limb	<i>t</i> =1.98 2nd limb	<i>t</i> =4.12***	<i>t</i> =2.37*	<i>t</i> =1.52
Y.S.	<i>t</i> =0.95 2nd limb	<i>t</i> =0.73 1st limb	<i>t</i> =1.16	<i>t</i> =0.62	<i>t</i> =1.72
L.M.	<i>t</i> =0.56 2nd limb	<i>t</i> =4.86*** 1st limb	<i>t</i> =2.44*	<i>t</i> =4.1***	<i>t</i> =1.72
L.L.	<i>t</i> =0.66 1st limb	<i>t</i> =0.75 2nd limb	<i>t</i> =0.17	<i>t</i> =0.55	<i>t</i> =0.83
S.A.	<i>t</i> =0.67 2nd limb	<i>t</i> =0.04 1st limb	<i>t</i> =0.67	<i>t</i> =1.17	<i>t</i> =0.34
P.B.	<i>t</i> =0.06 2nd limb	<i>t</i> =3.42** 1st limb	<i>t</i> =2.42*	<i>t</i> =1.13	<i>t</i> =2.24*

a significant difference in the final level of the first and second learning processes, the first learning process was found to be more intensive (i.e., the final MA and MV levels were lower). Upon comparing the final level reached in the second learning process with that reached in the first, it therefore turned out that the original learning session did not facilitate the second one.

Discussion

The decrease in the maximum amplitude and velocity of the postural forearm's upward shift occurring after unloading when the unloading is triggered by the subject's other arm lifting movement has been analyzed by Paulignan et al. (1989), and the role of the feedback and feed-forward postural adjustments involved in this kind of acquisition has been described (Forget and Lamarre 1990). One of the more general aims of the present study was to investigate whether any transfer of this learning is possible. The results indicate on the whole a lack of transfer, judging from the comparison made between the first series of the transfer learning session and the last series of the original learning session. In addition, the second (transfer) learning process was not faster than the first

one: the final level of the unloading amplitude and velocity in the third series either did not differ between the first and second learning sessions or was greater in the initial learning session (in the case of five subjects). With the number of subjects available in the present series, we did not observe any very marked differences in the intensity or level of the original and second transfer learning sessions depending on the motor dominance or on the sequence of the sessions (i.e., on whether the postural forearm was dominant or nondominant in the first session). Nor was the presence of motor asymmetry found to conspicuously affect the transfer.

This result is quite surprising at first sight. The anticipatory postural adjustments are specific to each movement and are closely associated with the performance of the movement. In the present paradigm, due to the presence of a symmetrical coordination, where the postural forearm becomes the moving arm and vice versa, one might have expected transfer learning to occur and to reduce the number of trials needed to reach the same score as during the original learning session. If the present result is confirmed with other types of anticipatory postural adjustments, this will indicate that the learned posturokinetic skills are not transferred and need to be relearned in the case of symmetrical movements.

Why was a lack of transfer noted in the present task? Transfer of skills learned by one hand has been reported to occur, mainly in structured sequences (see Cohen et al. 1990; Parlow and Dewey 1991), but also after specific isometric training (Weir et al. 1994). The first possible explanation for the lack of transfer might be that, since the coordinated task is a bimanual one, there may be an interference between the activities on the both sides, which may prevent the transfer, as described by Hicks et al. (1982). These authors interpreted this result in the frame of the motor overflow theory, whereby the untrained hand/hemisphere receives a form of passive training as a result of a subthreshold stimulation of the homologous musculature during initial training with the other limb and that dual engrams are formed. The interfering task would then prevent the formation of the second engram. The findings of Hicks et al. (1982) were not duplicated, however, by Parlow and Dewey (1991) using a sequential tapping task, when the other hand was engaged in an unrelated activity. Although the unrelated activity did not prevent the transfer when it was performed during the original learning session, it did prevent the transfer when it was performed during the transfer test trials.

Another possibility might be that the anticipatory postural adjustments belong to a different category of skills from those previously investigated, which involved sequential tapping tasks, and that their transfer learning might be differentially organized¹. Although transfer of the sequential tapping task is probably organized at the cortical level, the anticipatory postural adjustment might be organized at subcortical level. One should remember that the anticipatory postural adjustments in the bimanual load-lifting task persist after callosal section (Viallet et al. 1992). Other everyday activities involving highly trained bimanual coordination, such as lacing the shoes, have been reported in split-brain patients (see Trevarthen 1990; Geffen et al. 1994; Sauerwein and Lassonde 1994). The network in charge of the anticipatory postural adjustments is probably subcortical (see Gahery and Massion 1981; Alstermark et al. 1987; Ioffé et al. 1988; Birjukova et al. 1989; Horak et al. 1989; Luccarini et al. 1990). Although it seems likely that transfer might possibly occur at some subcortical level, for example through the cerebellum, evidence for such transfer in the case of anticipatory postural adjustments is lacking.

Acknowledgements The authors wish to thank M. Coulmance for her major contribution to the programming, and E. Kushnir for her help in data analysis. This work was supported partly by the Russian Foundation of Fundamental Research (project 93-04-06267) and by the French Ministry of Research and Technology. The English manuscript was revised by Dr. Jessica Blanc.

¹ A lack of transfer between the right and left hand trajectories during adaptation to Corioli forces was recently reported (Motor adaptation to Corioli force perturbation of reaching movements: endpoint but not trajectory adaptation transfers to the non exposed arm. Dizio P, Lackner JR, *J Neurophysiol* (1995) 74:1787–1792). By contrast, a transfer concerning the adaptation to the target location was present

References

- Astermark B, Lundberg A, Pinter M, Sasaki S (1987) Subpopulations and function of long C3–C5 propriospinal neurones. *Brain Res* 404:395–400
- Angel RW, Eppler W, Iannone A (1965) Silent period produced by unloading of muscle during voluntary contraction. *J Physiol (Lond)* 180:864–870
- Birjukova EV, Dufosse M, Frolov AA, Ioffe ME, Massion J (1989) Role of the sensorimotor cortex in postural adjustments accompanying a conditioned paw lift in the standing cat. *Exp Brain Res* 78:588–596
- Cohen A, Ivry RI, Keele SW (1990) Attention and structure in sequence learning. *J Exp Psychol Learn Mem Cogn* 16:17–30
- Dufossé M, Hugon M, Massion J (1985) Postural forearm changes induced by predictable in time or voluntary triggered unloading in man. *Exp Brain Res* 60:330–334
- Forget R, Lamarre Y (1990) Anticipatory postural adjustment in the absence of normal peripheral feedback. *Brain Res* 508:176–179
- Gahery Y, Massion J (1981) Coordination between posture and movement. *Trends Neurosci* 4:199–202
- Geffen GM, Jones DL, Geffen LB (1994) Interhemispheric control of manual motor activity. *Behav Brain Res* 64:131–140
- Hicks RE, Frank JM, Kinsbourne M (1982) The locus of bimanual skill transfer. *J Gen Psychol* 107:277–281
- Horak EB, Shupert CL, Mirka A (1989) Components of postural dyscontrol in the elderly: a review. *Neurobiol Aging* 10:727–738
- Hugon M, Massion J, Wiesendanger M (1982) Anticipatory postural changes induced by active unloading and comparison with passive unloading in man. *Pflugers Arch* 393:292–296
- Ioffe ME, Ivanova NG, Frolov AA, Birjukova EV, Kiseljova NV (1988) On the role of motor cortex in the learned rearrangement on postural coordination. In: Gurfinkel VS, Ioffé ME, Massion J, Roll J-P (eds) *Stance and motion: facts and concept*. Plenum, New York
- Luccarini P, Gahery Y, Pompeiano O (1990) Cholinceptive pontine reticular structures modify the postural adjustments during the limb movements induced by cortical stimulation. *Arch Ital Biol* 128:19–45
- Massion J (1992) Movement, posture and equilibrium: interaction and coordination. *Prog Neurobiol* 38:35–56
- Parlow SE, Dewey D (1991) The temporal locus of transfer of training between hands: an interference study. *Behav Brain Res* 46:1–8
- Parlow SE, Kinsbourne M (1989) Asymmetrical transfer of training between hands: implications for inter-hemispheric communication in normal brain? *Brain Cogn* 11:98–113
- Parlow SE, Kinsbourne M (1990) Asymmetrical transfer of Braille acquisition between hands. *Brain Lang* 39:319–330
- Paulignan Y, Dufosse M, Hugon M, Massion J (1989) Acquisition of co-ordination between posture and movement in a bimanual task. *Exp Brain Res* 77:337–348
- Sauerwein HC, Lassonde M (1994) Cognitive and sensori-motor functioning in the absence of the corpus callosum: neuropsychological studies in callosal agenesis and callosotomized patients. *Behav Brain Res* 64:229–240
- Seber GAF (1977) *Linear regression analysis*. Wiley, New York, Chapt 6
- Trevarthen C (1990) Integrative functions of the cerebral commissures. In: Boller F, Grafman J (eds) *Handbook of Neuropsychology*, vol 4. Elsevier, Amsterdam, pp 49–83
- Viallet F, Massion J, Massarino R, Khalil R (1992) Coordination between posture and movement in a bimanual load lifting task: putative role of a medial frontal region including the supplementary motor area. *Exp Brain Res* 88:674–684
- Weir JP, Housh TJ, Weir LL (1994) Electromyographic evaluation of joint angle specificity and cross-training after isometric training. *J Appl Physiol* 77:197–201