Effects of body immersion on postural adjustments to voluntary arm movements in humans: role of load receptor input

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1. The effect of body immersion on postural adjustments was studied in ten healthy subjects. Reaction times, for pushing or pulling a rigid handle, in response to a visual stimulus were measured. In addition EMG recordings were taken from upper arm and lower leg muscles during three levels of body immersion while standing on a platform (immersed to spinal levels: lumbar nerve root 2 (L2); thoracic nerve root 4 (T4); and cervical nerve root 7 (C7)), while floating and while standing or sitting out of water.

2. With increasing levels of body immersion there was a near linear reduction in the amplitude of the gastrocnemius (GM) EMG activity before (200 ms) the onset of a force signal from pulling, but immersion had a significantly weaker effect on the amplitude of the tibialis anterior (TA) EMG during pushing movements. There was no significant difference in the effect of body immersion on biceps femoris (BF) and rectus femoris (RF). Under free-floating conditions postural adjustments did not occur in response to pull or push movements. There were no adaptational changes of EMG adjustments during successive trials at a given immersion level.

3. Under non-immersed conditions reaction times were significantly shorter during sitting than during standing. This difference is assumed to be due to the postural adjustments required while standing before the onset of a voluntary arm movement. While standing, reaction times were significantly longer for pull compared with push movements. Under all conditions of body immersion the reaction times remained longer compared with the sitting condition, even when no leg muscle EMG adjustments were present.

4. It is assumed that the differential effect of body immersion on the antagonistic leg muscles is due to the differential neuronal control of antagonistic leg muscles with a strong influence from proprioceptive input (most probably from load receptors) on the leg extensors. The longer reaction times seen during body immersion, where no postural adjustments were evident, suggests that a supraspinal command to the leg muscles precedes the voluntary arm movement. However, because of the changed/decreased afferent input no postural adjustments are generated.

During standing and locomotion in humans any voluntary movement of the upper limbs requires an anticipatory postural adjustment prior to the execution of that movement in order to stabilize body equilibrium (Aruin & Latash, 1995; for reviews see Massion, 1992; Dietz, 1992). Although there is a large amount of literature regarding the behaviour of these postural reactions under different motor conditions, both from healthy subjects (see Massion, 1992) and from patients with movement disorders (see Dick *et al.* 1986), the origin of and the neuronal substrate underlying these postural responses remain unclear. It has been suggested that supraspinal commands are responsible for the early activation of the appropriate leg muscles prior to arm muscle activation (Gahery & Massion, 1981; Bouisset & Zattara, 1987). However, clear evidence for such a mechanism has yet to be shown.

The aim of this study was to investigate further the interaction between voluntarily induced commanded and automatic postural responses by analysing the postural reactions associated with pull and push arm movements in a reaction time task during different levels of body immersion. Under such conditions of partial body unloading actual body weight becomes reduced. Nevertheless, to maintain body equilibrium, the reactive forces associated with the push/pull movements (which under normal conditions are compensated for by postural pre-adjustments, i.e. before the onset of voluntary movement) remain constant. Therefore theoretically, leg muscle activation should remain unaffected

by body immersion despite the viscosity of the water which dampens body movement. Indeed, earlier experiments have shown that the compensatory reactions following a displacement are barely affected by body immersion *per se*, but rather depend upon the actual body weight (Dietz, Horstmann, Trippel & Gollhofer, 1989). The immersion experiments should answer the following questions. (1) To what degree do postural responses change with body immersion? (2) Is there differential behaviour of leg flexor and extensor muscles to such a change in the actual body weight? (3) Are there adaptational changes to unloaded conditions during successive trials? (4) Is there an influence of body immersion on reaction time? It is hypothesized that body immersion leads to a new pre-setting of the spinal neuronal mechanisms underlying postural responses.

METHODS

General procedures and recording methods

With the permission of the local ethical committee and the informed consent of the volunteers, postural reactions, associated with isometric arm pulling and pushing movements, were tested in ten healthy subjects (age 25·6 ± 4 years, mean ± S.D.) during partial body immersion. The subjects stood in an upright posture in individually adapted rubber shoes which were attached to an adjustable force platform. The platform was built within a cylindrical water tank which enabled the subject to stand out of water or to undergo full body immersion (see Fig. 1). In different experiments, the subjects were free floating in the tank, but were held in a vertical position by a load (3 kg) attached to the feet. Water temperature was maintained at 34 °C. A rigid handle was positioned at shoulder height in front of the subject. The handle was connected to a strain gauge allowing recording of the force exerted during the pushing and pulling movements. Above the handle were two light-emitting diodes, one green and the other red. The subject was asked to have his/her hand close to the handle and to push or pull the handle as quickly and as strongly as possible when the green or red light, respectively, was switched on. The lights were presented in a random order at time intervals between 4 and 7 s.

The pull and push arm movements were performed under three conditions of body immersion (water surface at spinal levels: L2 (standing); T4 (standing); and C7 (standing and floating)), and while out of the water as a control (standing (see Fig. 1) and sitting on a chair). These different conditions were applied in a random order. Each condition consisted of ten trials of both push and pull movements.

The EMG activity in the upper arm muscles (biceps brachii (BB) and triceps brachii (TB)) and the leg muscles (biceps femoris (BF), rectus femoris (RF), tibialis anterior (TA) and gastrocnemius (GM)) were recorded using surface electrodes which were isolated from the water using Opsite, transparent adhesive film (Smith and Nephew, Hull, UK). Ankle- and knee-joint movements were recorded by mechanical goniometers (custom-made) fixed at the lateral aspect of the ankle and knee (right leg). The forces exerted on the platform by the feet were recorded by Piezo-force transducers attached to the platform.

Data analysis

EMG recordings were amplified (microvolt amplifier; bandpass filter, 30–300 Hz) and were transferred together with the biomechanical signals to a microcomputer system via an analog-to-digital converter. All signals were sampled at 600 Hz. Every other trial out of ten trials in any given immersion condition was displayed (Fig. 1). After rectifying the EMG, the onset of the force signal (at time (t) = 1 s) produced by the voluntary arm movements was used as a trigger for averaging the EMG and biomechanical signals. The reaction time was determined by the time interval between the switching on of the light and the onset of the force signal. For a detailed description of the recording techniques and signal analysis, see recent articles by Dietz, Horstmann & Berger, 1989; Dietz, Colombo, Jensen & Baumgartner, 1995.

To investigate changes in EMG activity as a function of body immersion, the signal energy (root mean square, r.m.s.) was determined for a period before the onset of the force signal (−0·8 to 1 s). This was done because the most dramatic changes in leg muscle activation occurred at that time. The displacement of the body induced by the voluntary arm movements was determined from the ankle-joint goniometer signal for both push and pull movements.

The r.m.s. values of each muscle and subject were normalized to the mean values over all trials in one condition and subject. For the assessment of adaptational changes an analysis of variance was applied to find out any relationship between the normalized r.m.s. values and the number of trials within one experimental condition out of water or during immersion. In order to test for any difference in EMG activity or force between the different conditions a two-factorial analysis of variance was applied.

RESULTS

The postural reactions following the pulling and pushing of a rigid handle by the right arm during a visual reaction time procedure are shown in Fig. 1. This was done under both non-immersed (Fig. 1*A*) and fully immersed conditions (Fig. 1*B*). Every second trial of one condition is displayed.

While standing out of water (Fig. 1*A a*) there was a pre-activation of the gastrocnemius muscle about 200 ms before the onset of pulling force (at t = 1 s). Following onset of the force signal no GM EMG activity appeared. In contrast, when immersed (Fig. 1*Ba*), no significant pre-activation of the GM occurred. The BB activation started just prior to, or at the same time as, the force signal and was not modified by immersion. There was no visible change in leg or arm muscle activation during the course of the ten successive trials. The force applied to the handle was also unaffected by immersion.

Figure 1*A b* and *B b* shows the EMG patterns observed while pushing the handle. Under non-immersed conditions (Fig. 1*A b*) the pushing impulse was preceded by a tibialis anterior activation about 200 ms prior to the onset of the force signal (at t = 1 s) with a subsequent smooth decline in activity thereafter. There was also a triceps brachii pre-activation. There was no visible gastrocnemius (GM) activity in this condition (not shown). During immersion (Fig. 1*B b*), the upper arm muscle activation and the force signal remained constant. The TA pre-activity was not visibly changed in amplitude during body immersion. When evaluated systematically (see Methods) no adaptational change of leg or arm muscle EMG activity was found over twelve successive trials under any experimental condition tested.

Figure 2 shows the grand means (± S.D. for the out of water condition) of biceps and triceps brachii EMG activity during pull (Fig. 2*A*) and push (Fig. 2*B*) together with the forces exerted on the handle during the different experimental conditions. EMG activity in the arm muscles started 40–60 ms before the onset of the force signal and lasted over about 190 (BB) to 270 ms (TB). Arm muscle activation and force exertion on the handle was not affected by body immersion during pull and push movements (two-factorial analysis of variance).

Figure 3 shows the grand means (± S.D. for the out of water condition) of postural adjustments in upper and lower leg

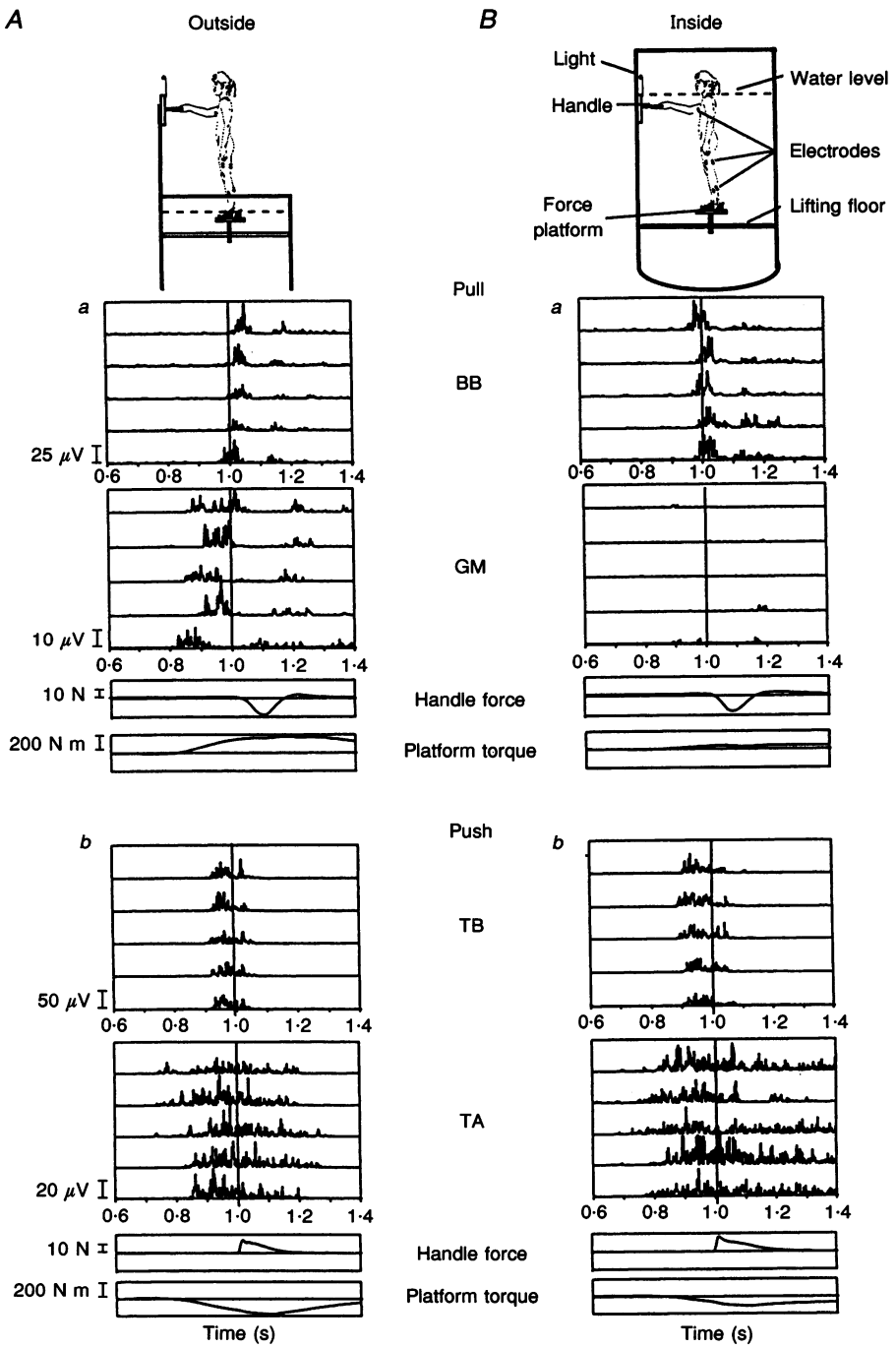

Figure 1. Experimental set-up

Electrophysiological and biomechanical signals from a subject standing out of water (*A*) and during immersion (C7 level, *B*) during pulling (*A a* and *B a*) and pushing (*A b* and *B b*) a handle. The schematic drawings above show the experimental set-up. Every other trial out of 10 trials of the rectified EMG of biceps brachii (BB) and gastrocnemius (GM) during pulling and triceps brachii (TB) and tibialis anterior (TA) during pushing a handle is displayed. Mean ($n = 10$) handle force and platform torque signals are displayed below the EMG recordings. The vertical lines indicate onset of the force signal ($t = 1$ s).

muscles during pull (Fig. 3*A*) and push (Fig. 3*B*) movements, together with the reaction forces acting on the platform at different immersion levels. Out of water the earliest activation of lower leg muscles started around 400 ms prior to the onset of the force signal and reached maximal amplitude around the onset of force (TA) or 80 ms before the onset of force (GM). With increasing body immersion GM pre-activation was reduced and became successively smaller in amplitude. The reduction in EMG amplitude was associated with diminished reaction forces exerted by the feet on the platform. This resulted in larger body excursions following the arm movement (not shown here). In contrast, there was only a slight decay of TA EMG amplitude with increasing body immersion. There was no significant co-activation of the respective antagonistic leg muscle (not shown). In the thigh muscles the amplitude of pre-activity was generally small and little influenced by body immersion.

In Fig. 4*A* the absolute quantified EMG values of TA (push) and GM (pull) EMG adjustment are shown for five of the conditions used in this study. During floating the EMG amplitude was small in both the TA and GM. The different levels of immersion, however, had a differential effect on the EMG amplitude of TA and GM with an approximately linear decline being observed in the latter.

Figure 4*B* summarizes the quantified and normalized (to the condition out of water) results of postural adjustments during pull and push movements obtained from all subjects. The normalized, integrated TA and GM responses are shown for the two reaction time tasks during different levels of body immersion. During sitting out of water (not shown) and during free floating there was no significant activation of postural muscles. During the other conditions there was a postural TA activation during push and a GM activation during pull movements. The level of body immersion had a profound effect on the strength of leg muscle activity and this effect was different for the two muscles, i.e. for the two motor conditions. With respect to the pushing condition, while not immersed, the effect of body immersion on the level of TA pre-activity was moderate, except during free floating ($P < 0{\cdot}05$). In contrast to this, a pronounced effect of body immersion on the GM activation occurred ($P < 0{\cdot}05$). Taking the normalized data, the effect of the level of body immersion on the two muscles was significantly different (analysis of variance $P < 0{\cdot}05$). In respect to the thigh muscles (quantified data not shown) body immersion resulted in a weaker pre-activation which was significant for the RF ($P < 0{\cdot}05$) but not for the BF. No significant difference was found between the effects on the two muscles.

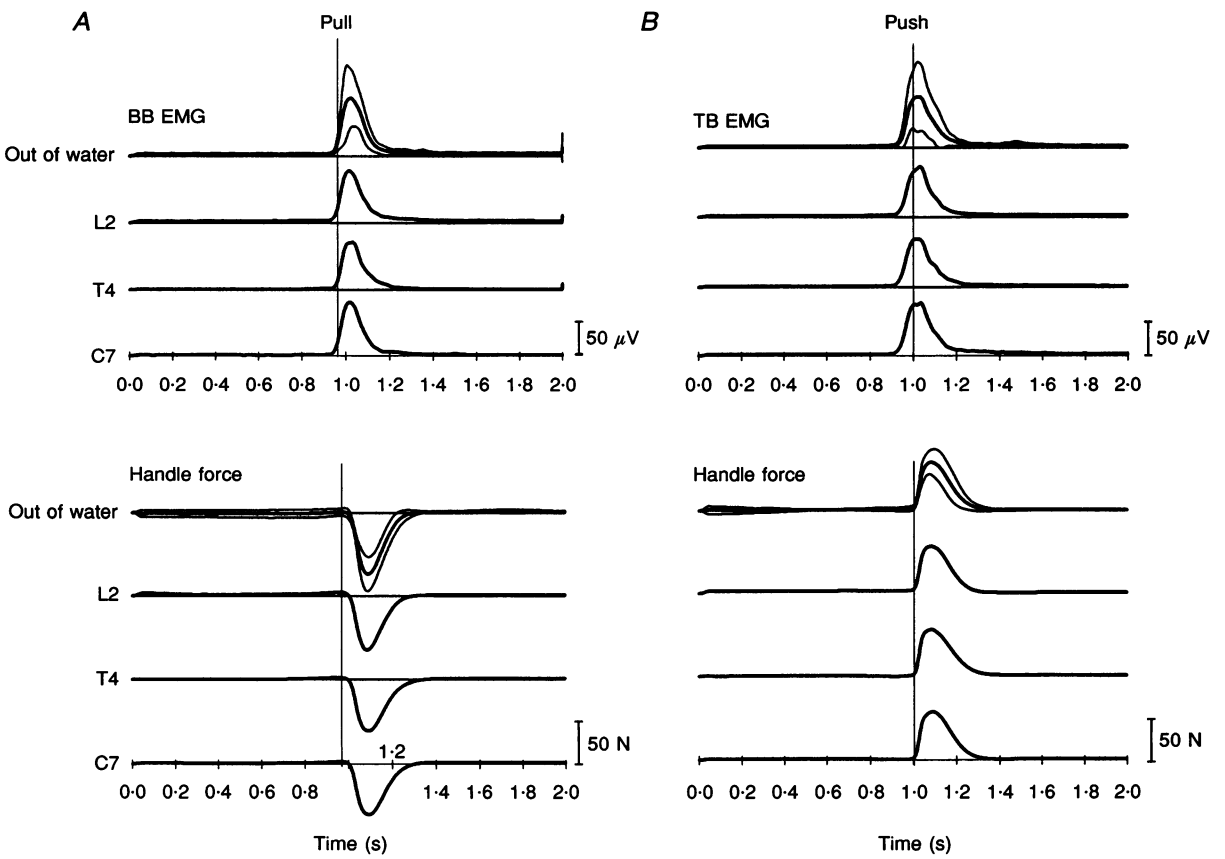

Figure 2. Upper limb muscle EMG and force

Means (± S.D. for out of water condition) of the rectified and averaged ($n = 10$) EMG activity (upper graphs) and handle force (lower graphs) during pulling (BB, *A*) and pushing (TB, *B*), while standing at different levels of body immersion. For explanation of vertical lines see Fig. 1.

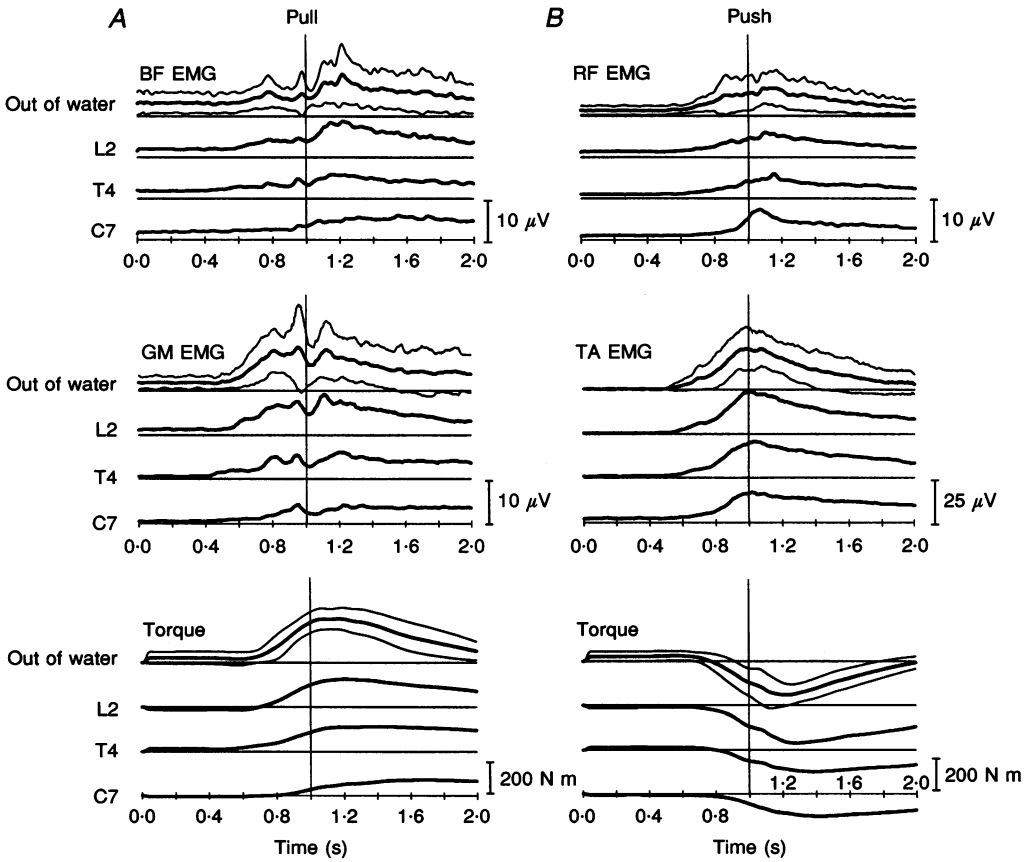

Figure 3. Postural adjustment and torque

Population means (± S.D. for out of water condition) of the rectified and averaged ($n = 10$) EMG adjustments in (from top to bottom) BF and RF muscles, GM and TA muscles and torques exerted by the feet on the forceplate during pulling (*A*) and pushing (*B*), respectively, while standing at different levels of body immersion. Note different calibration for TA. For explanation of vertical lines see Fig. 1.

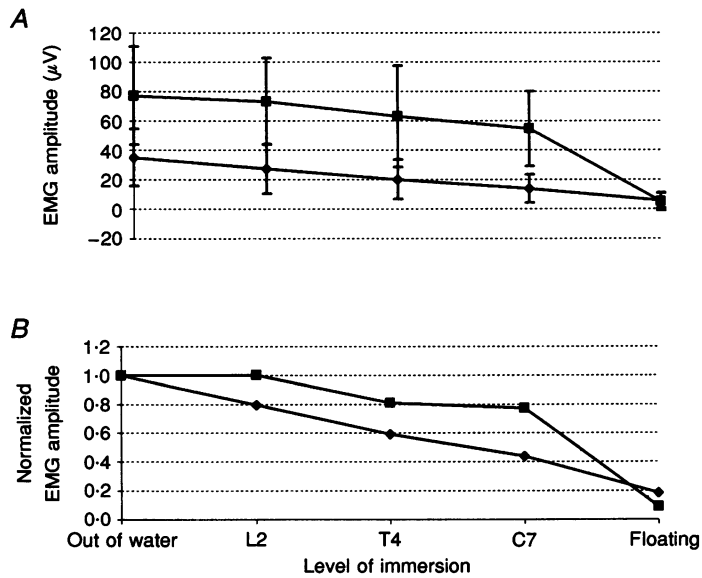

Figure 4. Quantified postural adjustment

Quantified GM (◆) and TA (■) EMG adjustments from $t = 0{\cdot}8$–$1{\cdot}0$ s obtained from all subjects during pulling and pushing, respectively, while out of water, during different levels of body immersion, and during free floating. *A*, absolute values of the mean EMG signals (± S.D.). *B*, data normalized to the standing out of water condition.

Body posture was more erect during immersion, i.e. subjects tended to lean slightly backwards prior to initiation of arm movements compared with standing out of the water. The effect of this change in body posture on GM activation was further analysed. Subjects exerted a mean static torque on the forceplate of about 15 N m when standing out of the water, and 0 N m during immersion (C7). The latter value was calculated to be 1·5 N m if body inclination was the same as standing out of the water. Body inclination was determined in addition by a potentiometer measuring the angle between forceplate and axis of the body. The pull/push movements were repeated in nine subjects standing out of the water with body posture (according to the torque and ankle angle) corresponding to that during body immersion (C7). By monitoring torque and ankle angle subjects could adopt identical body posture. In this new condition GM activation during pull movements was not significantly changed (Student's t test).

In Fig. 5 the absolute values of the reaction times are displayed. When differences between the different conditions were calculated by analysis of variance (see Methods) it was observed that during sitting the reaction times were significantly shorter compared with all other conditions ($P < 0·05$). This was true for the push as well as for the pull movements. The difference was, however, significantly more pronounced for the pull movements ($P < 0·05$). The differences in reaction times for pulling and pushing movements while sitting or standing were 78 ($P < 0·05$) and 46 ms ($P < 0·05$), respectively (mean reaction times during pull movements were 503 ± 136 ms for sitting and 581 ± 144 ms for standing out of water; mean reaction times during push movements were 507 ± 152 ms for sitting and 553 ± 154 ms for standing out of water). Reaction times tended to be shorter during the different levels of body immersion and longer during floating compared with the standing out of water condition (mean reaction times during pulling were 556 ± 164 ms for L2–C7 immersion and 584 ± 175 ms for floating; mean reaction times for pushing were 536 ± 144 ms for L2–C7 immersion and 595 ± 177 ms for floating). These differences were, however, not significant (analysis of variance).

DISCUSSION

The aim of the present study was to evaluate the influence of body immersion on the postural reactions associated with arm pushing and pulling movements on a handle. The postural reactions are needed in order to stabilize the body before the onset of the force acting on the handle and the body. Unloading of the body resulted in the following observations. (1) The compensatory postural reactions seen in the TA, associated with arm pushing movements, were less affected by body immersion than those of the GM during pulling movements. (2) There were no adaptational changes during successive trials in any one of the experimental conditions. (3) Reaction times were shorter during sitting than during standing or in any one of the immersion conditions.

These observations will be discussed with respect to the origin and generation of the postural responses associated with voluntary arm movements, the interaction between the voluntary arm muscle activation and the postural responses which appear automatically, as well as the functional implications arising from the behaviour of these responses.

Differential role of antagonistic leg muscles

The influence of the level of body immersion on postural adjustments was different for the antagonistic lower leg muscles, i.e. it was considerably greater on the leg extensor compared with the leg flexor muscles. This was still the case when the backward inclination of body posture during immersion was taken into account. This indicates a different susceptibility to a changed proprioceptive input and consequently, a different neuronal control of antagonistic leg muscles. The stronger influence of body immersion on the leg extensors, i.e. the antigravity muscles, is in agreement with the assumption that this activity is predominantly modulated and controlled by proprioceptive input (Dietz, Quintern & Sillem, 1987). The present experiments also suggest that the information from receptors, presumably in the leg extensors, signalling the presence and strength of contact forces, are of crucial importance for the strength of leg extensor activation. This result agrees with earlier

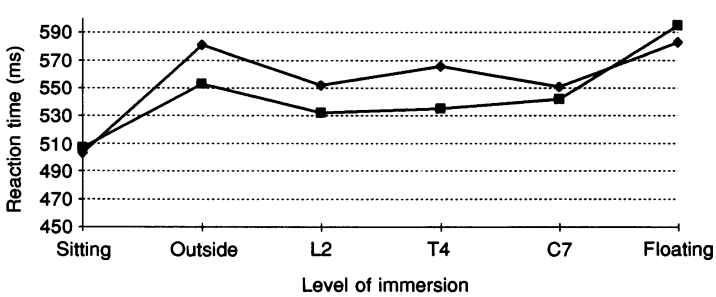

Figure 5. Reaction time

Mean visual reaction times obtained from all subjects for pulling (◆) and pushing (■), respectively, during sitting, standing out of water, different levels of body immersion, and free floating.

observations in the cat (Duysens & Pearson, 1980; Pearson & Collins, 1993) and man (Dietz, Gollhofer, Kleiber & Trippel, 1992), which stressed the functional significance of extensor load receptors during stance and gait. The weaker GM postural adjustments during body immersion resulted in reduced reactive forces exerted by the feet. This effect was obviously not compensated for by a stronger activation of upper leg muscles but rather by a combination of both damping by water viscosity and larger body excursions.

The lesser effect of body immersion on the leg flexor muscles may be due to their different neuronal control. It has been suggested that these muscles are predominantly activated and controlled by central mechanisms (Dietz *et al.* 1987). Such a different neuronal control would fit with the suggestion that there are stronger connections of supraspinal motor centres to the leg flexor than to the extensor muscles (Brouwer & Ashby, 1992) and a stronger cortical control of leg flexors during visual tasks in cat (Beloozerova & Sirota, 1988) and man (Dietz, Schubert & Trippel, 1992).

During both pulling and pushing tasks there were no adaptational changes in postural adjustments during body immersion. At a given immersion level, the amplitude or duration of TA or GM postural adjustment did not change during successive trials. Therefore, no reflex adaptation took place as it has been suggested for other postural reactions (Nashner, 1976). This implies that the setting for the postural response has been changed already before the first trial was executed, presumably due to an appropriately changed afferent input.

Postural adjustment and reaction time

The observation that reaction times were shorter while sitting than while standing can probably be attributed to the fact that automatic postural adjustments have to precede voluntary arm movements. During sitting only the trunk has to be stabilized before voluntary movement starts which requires shorter pathways for adjustment. The difference of about 50 ms in reaction time would fit with the time required for a feedback loop including the activation of leg muscles for postural adjustment before execution of the voluntary task. The difference in reaction time between sitting and standing was, however, larger when the GM had to be activated. This may be due to the differential neuronal control of the extensor muscles compared with the flexors which are under predominantly central control (see above). In the latter case this control facilitates matching the postural adjustment with the voluntary movement command. In contrast, activation of leg extensors, as the main anti-gravity muscles, depends predominantly on input from 'load receptors' (for review see Dietz, 1992). In this case matching of GM activation with the voluntary command might require more time for an adequate adjustment.

When the push/pull movements were performed during full or almost full immersion, no postural adjustments could be observed. Nevertheless, reaction time showed a tendency to become longer. This observation suggests that in the latter condition a signal from the cortex to the leg muscles precedes the pull/push movements (cf. Palmer, Downes & Ashby, 1996) and therefore delays the onset of arm muscle activation. The postural adjustment induced by the supra-spinal signal is however, masked by the fact that additional afferent signals are needed to signal the presence and strength of contact forces in order to generate the appropriate degree of leg muscle EMG activity for postural adjustment.

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