Adaptive Changes in Anticipatory Postural Adjustments With Novel and Familiar Postural Supports

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Hall LM, Brauer S, Horak F, Hodges PW. Adaptive changes in anticipatory postural adjustments with novel and familiar postural supports. J Neurophysiol 103: 968–976, 2010. First published December 2, 2009; doi:10.1152/jn.00479.2009. Anticipatory postural adjustments (APAs) serve to stabilize posture prior to initiation of voluntary movement. This study examined the effects of changes in postural support on APAs using novel and familiar support paradigms. We also investigated whether postural strategies were refined with practice and how the CNS responded when multiple supports were available. Twelve healthy subjects stood on dual force platforms and performed 20 randomized left and right rapid leg-lift tasks in response to a visual cue under four conditions: unsupported, bilateral handgrip, bite plate, and a combined handgrip and bite plate condition. Vertical ground reaction forces, electromyography of limb, trunk and jaw muscles, and forces exerted on the support apparatus were recorded. Shift in center-of-pressure amplitude and duration were reduced with increased support. Muscles were recruited in advance of the focal movement when able to contribute to stability, and activity was modulated based on the amount of support available. The CNS adapted anticipatory postural strategies immediately with changes in condition regardless of familiarity with the support; however, adaptation was only complete at the first repetition in conditions that involved familiar support strategies. Tasks that involved a novel bite strategy continued to adapt with practice. In the multiple support condition, both hand and bite strategies were immediately incorporated; however, the contribution of each was not identical to conditions where supports were provided individually. This study emphasizes the flexibility of the CNS to organize postural strategies to meet the demands of postural stability in both familiar and novel situations.

INTRODUCTION

Voluntary movements are generally accompanied by anticipatory postural adjustments (APAs) that are matched to the postural demands of a predictable task (Belen’kii et al. 1967; Cordo and Nashner 1982). APAs are dynamic events, preplanned by the CNS, that serve to counteract the challenge to postural control induced by predictable perturbations (Arutyunyan et al. 1969) such as those that accompany volitional limb movements. Previous studies have shown that APAs are scaled by the degree to which movement is expected to disturb postural equilibrium. For example, when the postural challenge is greater, the duration of the APA is increased (Bouisset 1991; Bouisset and Zattara 1981). This suggests that the CNS plans a specific sequence of muscle activity to counteract expected postural perturbations and alters the timing and magnitude of the initial postural adjustments in association with changes in postural demands based on experience with similar movements (Horak et al. 1989). It follows that familiar tasks such as hand grasp and finger touch would alter APAs and result in inclusion of use of those body segments in the postural preparation (Slijper and Latash 2000), but it is unclear whether novel strategies that are unfamiliar to an individual (e.g., the potential to use jaw muscles) can elicit similar changes.

Properties of APAs change with variation in postural support. APA amplitude is reduced when posture becomes more stable (e.g., when additional support is available) (Cordo and Nashner 1982; Nardone and Schieppati 1988) and when APAs are less helpful, for example in unipedal posture or standing on a movable platform that reduces the potential for ankle torque to assist postural recovery (Gantchev and Dimitrova 1996; Nouillot et al. 1992). Addition of hand support, which is a common strategy to increase postural stability, reduces the postural response of leg muscles and increases those of arm muscles (Slijper and Latash 2000). The effect of unfamiliar and multiple external supports on APA timing and amplitude are not known. If the nervous system is presented with a new solution to simplify postural control, but for which there is no prior experience (i.e., use of the jaw for postural stability), the nervous system may either predict its utility and integrate it into a new postural strategy or leave the postural preparation unchanged. If maintenance of equilibrium is the primary goal of the CNS, we hypothesize that any muscle able to contribute to stability could be recruited in advance of the volitional movement task.

Adaptation of postural responses involves changes in both timing and amplitude of APAs with repeated performance of the motor task (Friedli et al. 1984). Feedback of performance from previous trials allows the CNS to optimize performance of subsequent trials. There is conflicting evidence whether further adaptation in postural responses occurs after the first repetition and, if present, the rate at which it occurs. Studies of postural reactions to repeated externally applied perturbations have reported rapid adaptation within the first few trials (Cordo and Nashner 1982), slow adaptation (Hansen et al. 1988), and no adaptation (Diener et al. 1984) after the initial presentation of a new condition. Furthermore, Maki and McCroey (1997) showed that APAs, determined from changes in center of pressure (COP), were absent in the initial compensatory stepping response to an external perturbation but emerged when participants became familiar with the characteristics of the perturbation. It remains unknown how the CNS adjusts...
motor commands, and therefore APAs, to optimize postural stability in voluntary movements. We hypothesized that conditions that involve a familiar support strategy will undergo limited adaptation after the first repetition as the nervous system will have been exposed to the utility of the additional postural support previously and be able to predict how to integrate the new body segments into the postural preparation. We also hypothesized that conditions in which novel supports are used would require considerable adaptation after the initial trial as a result of trial and error.

This study aimed to examine how changes in support, both novel and familiar, affect APAs and to determine whether postural strategies are refined with practice. In addition, we aimed to investigate the response of the neuromuscular system when more than one external support was available.

**METHODS**

Subjects

Twelve right-hand dominant healthy individuals [4 male and 8 female, age: 25 ± 6 (SD) years, height: 168 ± 9 cm, weight: 61 ± 15 kg] participated in this study. Subjects were excluded if they had a history of neurological, respiratory, circulatory, or vestibular disorders, previous fractures/surgery to the spine, limbs, and face, recent or current pregnancy, or gross postural deformities or if they wore dentures. All procedures conformed to the Declaration of Helsinki, and the study was approved by the Institutional Medical Research Ethics Committee.

Kinematic and kinetic data

Acceleration of the lower limbs was measured using triaxial accelerometers (±3 G, sensitivity 360 mV/G, Dimension Engineering) attached to the left and right anterior surface of the patella with the x axis aligned to the vertical axis of the body. The vertical component of ground reaction forces \( F_z \) of the lower limbs were recorded using two force plates (Bertec, Model No. 4060-70-4000). Force plate and acceleration data were sampled at 2,000 Hz.

Subjects wore a head-mounted laser that pointed to an infrared-sensitive target board. The target provided audible feedback when the laser moved outside a 90-mm-diam target zone. Hand and jaw forces were recorded using custom-made strain gauge hand grips (grip width: 64 mm, range: 20 kg, sensitivity: 2.25 mV/V, CCT Transducers) and bite plates (occlusal distance: 15 mm, gauge resistance: 120 \( \Omega \), strain range: 4%, RS Components) mounted to a support frame. A force transducer (range: 250 lb, sensitivity: 3.00 mV/V, Scale Components) on the support frame recorded forces applied to the frame that could not be attributed to pure grip and bite forces, for example if subjects leaned on the hand grips/bite plate. The bite plate was positioned to allow the subject to maintain their natural upright posture and top of the hand grips were adjusted to the height of the acromion (Fig. 1).

Electromyography

Electromyographic (EMG) activity of right-sided jaw muscles and bilateral trunk and limb muscles was recorded using surface electrodes. Disposable self-adhesive dual electrodes (10-mm-diam Ag/AgCl disks, interelectrode distance: 20 mm, Noraxon) were placed over the oblique externus abdominus (OE) (Ng et al. 1998), tibialis anterior (TibA), masseter (MAS), digastric (DIG), and the lumbar erector spinae (LES) ~4 cm lateral to the L1 spinous process. Electrodes were also placed on the body bellies of the biceps brachii (BicB), triceps brachii (TricB), long finger flexors (FingF), and gastrocnemius lateralis (GastL) (Cram et al. 1998).

**Procedure**

We examined the effect of increased postural support on APAs associated with a hip flexion task in four conditions performed in random order: unsupported (US), bilateral hand grip (HG), bite plate (BP), and combined hand grip and bite (HG+BP). Subjects stood with feet 10 cm apart on separate force plates for all conditions, 1.5 m from the target board, and were instructed to relax before initiation of trials (Fig. 1). The starting position for conditions required participants to either: stand unsupported with no contact with the support frame (US); loosely hold the hand grips (HG); rest with the bite plate making contact with the teeth (BP); or both hand grips and bite plate support (HG+BP). In all conditions, subjects were asked to “lift their left or right leg, as fast as possible, in response to the randomized left or right visual cue while attempting to keep the laser within the white target region.” An infrared light beam gave an auditory signal when the lifted leg reached ~75° hip flexion, following which the leg was returned to the starting position. A head-laser target was provided to ensure head position remained similar for conditions in which the head was constrained (BP and HG+BP) and those in which the upper body was free to move (US and HG). No instructions were given as to how to use the hand grips and bite plate. Twenty correctly performed repetitions were completed per condition with a minimum of 10 s between repetitions to allow subjects to resume a relaxed standing posture with equal weight distribution. Trials in which the incorrect leg was lifted or there was hesitation in initiation of movement were rejected and repeated. Subjects rested for 3 min between conditions to minimize the potential for fatigue.

**Data analysis**

Control of voluntary movement consists of a focal component that involves movement of body segments and a postural component that provides whole body stabilization (Gelfand et al. 1966). Lower limb flexion during upright standing is a complex paradigm to analyze as there is no clear distinction between the postural and focal compo-
nents, and it involves a transitory base of support (Do et al. 1991; Nouillot et al. 1992; Rogers and Pai 1990). To increase the clarity of interpretation of results due to changes in base of support, we analyzed all forces exerted on the body from the physical environment as well as EMG data (Bouisset and Do 2008).

To eliminate the potential for experimenter bias, data were coded by a research assistant and presented with no indication of condition. Accelerometer and force plate data were low-pass filtered at 30 Hz (4th-order Butterworth). Similar to gait initiation, the APA was characterized by an initial mediolateral shift in COP toward the lifted leg followed by a shift toward the stance limb prior to foot off. Thus the APA was characterized by an increase in vertical force ($F_z$) under the leg to be lifted as center of mass shifted toward the stance limb. For each repetition, three clearly defined timing characteristics were visually identified from the force plate data on the side of the lifted leg: onset of $F_z$ increase; peak APA, and foot off (Fig. 2). Peak APA was identified as the peak $F_z$ of the lifted limb prior to unloading. Foot off was identified as the point at which $F_z$ of the lifted limb first reached zero. An anticipatory adjustment of ground reaction forces was considered absent in trials in which the initial change was a decrease in $F_z$ of the lifted limb, and an increase in $F_z$ of the stance limb. APA amplitude ($F_z$ peak minus $F_z$ at onset of increase) and duration (time of $F_z$ peak minus time of onset of $F_z$ increase) were calculated, as was leg lift reaction time (time of foot off minus time of visual trigger). To determine if the neuromuscular system further adapted the postural strategies after presentation of a new external support, the onset, amplitude, and duration of the APA were averaged over the first two (repetitions 1 and 2), middle two (repetitions 5 and 6), and last two (repetitions 9 and 10) repetitions of each leg movement.

EMG data were high-pass filtered at 50 Hz to remove movement artifact (4th-order Butterworth) and analyzed as amplitude in 30-20-ms epochs with 20 epochs (400 ms) before and 10 epochs (200 ms) after foot off. Epoch analysis was chosen due to the presence of ongoing background EMG activity, which made visual identification of EMG onsets difficult. EMG amplitude was calculated as root mean square (RMS) for each epoch, and data were normalized to peak amplitude across epochs and averaged over trials. Baseline EMG activity was defined as the average amplitude of the first three epochs (60 ms) of each trial (i.e., 340–400 ms before foot off) and onset of EMG as the 20-ms epoch in which the EMG increased significantly from the baseline (using ANOVA, see Statistical analysis). Time of peak EMG amplitude was determined from epoch data averaged across repetitions for each condition and subject.

Kinetic data from the hand grips, bite plate, and bar force (support apparatus) were analyzed both from raw data and the mean amplitude in epochs as per EMG data. Force amplitude was calculated from epoch data as the peak-to-peak force in each repetition due to the variable baseline forces between subjects. Time of peak force was also determined from epoch data, and the time of onset of force change was established from raw data using the approximated generalized likelihood ratio method of onset detection (Staude 2001). This method has been shown to be superior to onset detection using SD methods and was chosen as support apparatus force onsets were slower and therefore less easily defined visually. Force amplitude and onset of force in support apparatus were also averaged over the first two, middle two, and last two repetitions to determine if adaptation occurred.

**Statistical analysis**

Statistical analysis was performed using Statistica 7 (Statsoft). Reaction time and the onset, amplitude, and duration of the anticipatory increase in $F_z$ under the leg to be lifted were compared between conditions using a repeated-measures ANOVA. Amplitude of EMG and force data were compared between epochs and conditions, and time of force onset in support apparatus compared between conditions using repeated-measures ANOVAs. Adaptation data (onset, amplitude, and duration of the anticipatory increase in $F_z$ under the leg to be lifted and support apparatus force amplitude and onset) were compared between repetitions (average of 1st, middle, and last repetitions) and within conditions using a repeated-measures ANOVA. Post hoc testing was performed using Duncan’s multiple range test, and significance was set at $P < 0.05$.

**RESULTS**

**Changes in leg-lift task**

The reaction time from the visual stimulus to foot off differed between conditions (main effect: condition $P < 0.001$) and was shortest in conditions that included a familiar hand support strategy (post hoc: $P < 0.001$). Reaction times were slowest in the unsupported and BP conditions (Table 1), which were the same (post hoc: $P = 0.43$). Handgrip (HG) and combined HG+BP (post hoc: $P = 0.60$) were also similar.

Acceleration of the lower limbs differed between conditions (main effect: condition $P = 0.018$) and was greater during the US condition (Table 1) compared with HG (post hoc: $P = 0.028$) and HG+BP (post hoc: $P = 0.004$). Acceleration did not differ among HG, BP, and HG+BP (post hoc: $P > 0.15$), thus changes in APA duration and amplitude between the three support conditions cannot be explained by changes in leg acceleration.

**Force plate data**

As expected, there was an initial shift of COP toward the lifted limb prior to foot off. Onset of the shift in COP in the US

<table>
<thead>
<tr>
<th>Condition</th>
<th>Lower Limb Acceleration, ms$^{-2}$</th>
<th>Trigger to Onset APA</th>
<th>Trigger to Foot Off</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unsupported</td>
<td>14.0 ± 5.6</td>
<td>258 ± 50</td>
<td>736 ± 79</td>
</tr>
<tr>
<td>Hand grip</td>
<td>11.4 ± 6.0</td>
<td>287 ± 44</td>
<td>609 ± 67</td>
</tr>
<tr>
<td>Bite plate</td>
<td>11.4 ± 4.6</td>
<td>273 ± 43</td>
<td>752 ± 117</td>
</tr>
<tr>
<td>Hand grip + Bite plate</td>
<td>10.4 ± 6.2</td>
<td>313 ± 54</td>
<td>619 ± 74</td>
</tr>
</tbody>
</table>

Values are means ± SD.
condition, as determined from the increase in $F_z$ under the lifted leg, was initiated by $479\pm 82$ ms prior to foot off with an amplitude of $172\pm 69$ N (29% of body weight) and duration of $278\pm 29$ ms.

Amplitude and duration of the anticipatory shift toward the lifted leg (increase in $F_z$ under the lifted foot) were affected by support condition and were smallest and shortest in the condition with maximum support, HG+BP [amplitude $16\pm 17$ N; duration $68\pm 42$ ms], followed by HG, BP and US (Fig. 3). Duration of the anticipatory increase in $F_z$ differed between conditions (main effect: condition $P < 0.001$; post hoc: all: $P < 0.007$), and the $F_z$ increase differed between all conditions (main effect: condition $P < 0.001$, post hoc: $P < 0.001$) except HG+BP and HG (post hoc: $P = 0.36$).

Support apparatus data

Forces in all four support apparatus increased above baseline levels by 200 ms prior to foot off in conditions where specific support was available to contribute to stability (Fig. 4). Onset of the anticipatory increase in $F_z$ under the leg to be lifted was initiated prior to onset of any force support apparatus in any condition (main effect all: force $P < 0.001$, post hoc: all: $P < 0.004$), except HG+BP in which the onset of grip forces was not different to the onset of $F_z$ increase (post hoc: left grip: $P = 0.18$; right grip: $P = 0.39$). Conditions in which the bite plate could be used to assist postural recovery (BP and HG+BP) showed no difference in onset of forces between bite plate and bar force apparatus (post hoc: $P > 0.13$). Specific ordering of force apparatus onsets within individual trials and subjects was not evident. All subjects were right-hand dominant, and there was no difference between the onsets of left and right grip force in any condition (post hoc: $P > 0.57$).

Peak force amplitude in all apparatus was reached ~60 ms after foot off when the supports were available to provide postural stability. Time of peak amplitude of the bar force differed between conditions (main effect: condition $P = 0.009$) such that force amplitude reached its maximum earlier in HG than BP and HG+BP (post hoc: HG: $P = 0.006$; BP: $P = 0.016$). Left-handgrip force peaked earlier in HG+BP than the HG condition (main effect: condition $P = 0.013$), but there was no difference in time of peak force in the right-hand grip (main effect: condition $P = 0.92$).

Right grip force peak amplitude was greater in HG (in which hand grips were the only supports available) than HG+BP (main effect: condition $P = 0.029$). Peak hand grip amplitude was higher during left leg-lift tasks compared with right leg lifts (main effect: leg lift: $P = 0.039$) in the right hand grip. There was no difference in peak amplitudes between conditions in the left hand grip (main effect: condition $P = 0.64$), however greater force was observed during right leg compared with left leg tasks (main effect: leg lift $P = 0.007$).

EMG data

Only results from right-sided muscles are presented to reduce repetitiveness and confusion between ipsi- and contralateral leg lift tasks in relation to left- and right-sided muscles. Left-sided muscles responded in an identical manner with movement and were considered in the interpretation of muscle responses to left versus right leg lifts. As expected, in conditions in which specific body regions could not actively contribute to stability (e.g., jaw muscles in tasks with no bite plate), EMG activity of muscles in these regions did not change during leg lift tasks (Fig. 5). In trials in which muscles could contribute, they were recruited ≥300 ms in advance of foot off (Fig. 6). Trunk and lower limb muscles available to contribute to stability in supported and unsupported conditions showed changes in activation depending on the level of support available and the role played in completion of the task.

Right-sided facial muscles responded in a similar manner with left and right leg-lift tasks. Baseline and peak activity of DIG and MAS were increased in conditions where they were able to contribute to stability (interaction: condition*epoch DIG and MAS $P < 0.001$; post hoc: all $P < 0.007$, peak all $P < 0.001$) but showed no change from baseline in other conditions (post hoc: epochs: all $P > 0.07$; Fig. 7). DIG and MAS were co-activated in HG+BP and BP conditions, and activation was greater in the BP condition when bite was the only external support available (main effect: condition $P < 0.001$; post hoc: $P < 0.001$). Activity of DIG and MAS increased above baseline ~240 and ~320 ms before foot off, respectively, in the BP condition and ~100 and ~200 ms before foot off in the HG+BP condition.

Baseline EMG of arm muscles was not different between conditions except for BicB in which resting levels in the
HG+BP condition were greater than in conditions in which hand support was not offered (interaction: condition*epoch: P < 0.001; post hoc: P < 0.001; Fig. 7). Arm muscle responses differed between ipsilateral (right) and contralateral (left) leg lifts. In conditions where arm muscles were able to contribute to stability, EMG activity of the right BicB and FingF increased with left leg lifts (~280 ms prior to foot off) and reached peak amplitude at foot off and ~60 ms prior to foot off respectively, whereas the right TricB failed to rise above baseline levels. The opposite occurred with right leg lift tasks; activity of TricB increased but BicB and FingF remained at baseline levels. This suggests arm muscles differ from jaw muscles and show selective, lateralized activation, most likely in an attempt to control trunk rotation that accompanies unilateral leg lift tasks, which inherently display dynamic asymmetry. EMG data from BicB and FingF showed that these muscles were used in a similar manner within conditions, therefore only BicB is represented graphically (Figs. 6 and 7).

Ipsilateral leg lift tasks were generally associated with greater trunk muscle EMG than contralateral tasks. There was no difference in baseline EMG levels of trunk muscles between conditions (interaction: condition*epoch: P > 0.13). RMS EMG amplitude of OE and LES in right leg lift tasks (muscles ipsilateral to the lifted leg) reached peak amplitude ~20 and ~100 ms before foot off, respectively. LES activity in the HG and HG+BP condition did not change from baseline levels with the contralateral (left leg lift) task (post hoc: P > 0.06). OE peak RMS EMG amplitude was lower in BP compared with all other conditions (interaction: condition*epoch: P < 0.001; post hoc: P < 0.03) with right leg lifts. The peak amplitude of LES in ipsilateral tasks was greater in conditions in which hand grips were used (HG and HG+BP) (interaction: condition*epoch: P < 0.001; post hoc: P < 0.03) and coincided with large EMG activity in TricB.

The role of leg muscles differed between lower limb tasks. Lower limb muscles were most active in the lifted leg, and there was no difference in peak EMG activity in TibA with ipsilateral leg lifts. Peak RMS EMG activity of GastL in right leg-lift tasks was significantly lower in support conditions compared with US (interaction: condition*epoch: P < 0.001; post hoc: P < 0.04), and differed between support conditions with least activity in the condition of maximum support (post hoc: P < 0.05). TibA EMG reached its peak ~20 ms after foot off; whereas GastL reached its peak ~100 ms before foot off, consistent with the role of GastL in push off and that of TibA in elevation of the foot. Onset of GastL EMG activity was earlier in contralateral tasks (main effect: leg lift: P = 0.019) in which it contributed to stabilization of the stance limb.

**Adaptation**

The anticipatory increase in $F_z$ under the leg to be lifted showed adaptation by the first repetition of each condition compared with the US control task. Apart from the immediate change in anticipatory increase in $F_z$, there was no further adaptation in onset of $F_z$ increase relative to foot off (interaction: condition*repetition: P = 0.99), its duration (interaction: condition*repetition: P = 0.78), or amplitude (interaction: condition*repetition: P = 0.09) after the first repetition for any condition.

There was no further adaptation of force amplitude of any support apparatus after the first trial in the bite plate or left and right grip in any condition (main effect: repetition: P < 0.18). Analysis of bar force showed adaptation of force amplitude by the first repetition and with further repetitions in all conditions in which external support was available (main effect: repetition: P = 0.007). Bar force amplitude in the first two repetitions was less than middle and last repetitions for HG, BP, and HG+BP conditions (post hoc: repetition: P < 0.03). Taken together these data indicate that although the bar force amplitude changed, subjects did not increase the force applied to the bite plate or hand grips.

Analysis of onsets of force in the support apparatus across repetitions showed onset of bite force in the BP and HG+BP condition occurred earlier in initial repetitions than middle and
last repetitions (main effect: repetition: $P = 0.02$; post hoc: $P < 0.02$). There was no adaptation in the onset of force after the first repetition in the other support apparatus (main effect: repetition: $P > 0.66$).

**DISCUSSION**

The results of this study support our first hypothesis that the CNS adapts to use any available support, including those that are novel. The second hypothesis was also supported; the CNS adapts very quickly with no additional adaptation for familiar supports, and there is only minor additional adaptation when novel supports are available. Further, the data show that when multiple supports are available the CNS adjusts the relative contribution of each support.

**Changes in focal limb movement with changes in support**

Additional support in standing led to changes in focal movement of the leg. Lower limb acceleration decreased with postural support; however, the type of support had no affect. The slowing of focal leg movement is supported by a decrease in gastrocnemius EMG activity in the lifted limb, which would result in reduced push off force in conditions with additional support.

These data contrast with other studies that show increased velocity of voluntary movement in upper limb pointing (Yiou et al. 2007) and arm pull (Cordo and Nashner 1982) when support is increased. Greater leg lift acceleration in the current study when no additional support was available possibly reflects the need to re-establish a bipedal base of support as soon as possible; however, this is at the expense of a greater postural perturbation.

**Novel and familiar strategies are used to contribute to anticipatory postural adjustments**

It is important to emphasize that APAs can be defined with respect to EMG as well as to biomechanical variables (Bouisset and Do 2008). Reported effects of changes in support on the
anticipatory shift of COP have been inconsistent, partly due to the variation in investigation of these parameters. Previous work suggests anticipatory activity of leg muscles is reduced by both increased and decreased postural support. Nardone and Schieppati (1988) reported a complete disappearance of postural preparation in leg muscles when hand support was provided during voluntary rise-on-toes tasks compared with a free-standing condition. In contrast, other studies in which the base of support was reduced, thereby increasing postural instability and decreasing the potential for leg muscle activity to contribute to balance, also resulted in decreased anticipatory shifts in COP (Aruin et al. 1998; Nouillot et al. 1992; Pedotti et al. 1989). Thus leg muscle contribution can be adaptively reduced by either an increase or decrease of support.

In the current study, use of external postural support reduced the amplitude and duration of the anticipatory shift in COP (as evidenced from a decrease in $F_z$), i.e., less movement was required to counteract the destabilizing effect of the focal movement. The reduction in the shift of COP was closely associated with the type and amount of support available. As expected, the greatest shift in COP occurred in the unsupported condition. In that condition, the only strategy available to counteract the perturbation was to shift the body weight toward the stance limb, which was assisted by an initial loading of the leg to be lifted. This large COP shift could also be partly attributed to greater lower limb acceleration (and therefore greater reactive forces) in this condition. However, in the conditions with additional support, shifts in COP became less important as the postural response included a combination of shift in COP and support at the hand or jaw. These results are similar to those of Noe et al. (2003), who showed that hand grip forces assisted the ground reaction forces during voluntary movement to maintain postural equilibrium.

A comparison of the three support conditions showed that the novel bite condition involved greater changes in ground reaction forces than conditions that included a familiar hand strategy. It is not clear whether this is the result of unfamiliarity of the task, or, perhaps more likely, that the jaw was not able to provide the same level of postural support as the hands. Due to their moment arms and size, the large appendicular muscles, such as biceps and triceps brachii, are likely to have greater potential to influence trunk control than the small axially aligned jaw muscles. Also the shoulders are directly linked to the trunk, whereas the jaw forces are transmitted indirectly via the neck. Thus a greater shift in COP is likely to be required for lifting the leg with jaw support than with arm support.

There are a number of possible explanations for the involvement of jaw muscles in conditions where they were available to contribute to stability: to stabilize the head, to prevent movement of the bite plate in the mouth, to provide postural support for the body, or a combination of all three. Although there were only minor changes in APAs between the HG and HG+BP conditions, several factors support the notion that that the jaw response contributed to postural support. First, APA duration decreased in the HG+BP compared with the HG condition, which suggests the jaw affected anticipatory preparation. Sec-

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**FIG. 6.** Epoch analysis relative to foot off (•••) for rapid lower limb flexion. All epoch data are normalized to peak activity across conditions and displayed with mean and 95% confidence interval for each condition. ■, ▲, ●, ●, significant change of EMG activity from baseline levels. A: right leg lift, B: left leg lift.
ond, a comparison of these two conditions revealed increased peak gastrocnemius muscle activity in the hand only condition. This indicates that more push off was required when the jaw muscles were not available to participate in lateral weight shift that precedes foot off, which is an integral component of postural preparation.

Familiar, but not novel, strategies are fully adapted from the first repetition

With the introduction of additional postural support, the CNS immediately involved new upper extremity muscles in the postural response in the first trial. Hand support is common in everyday situations, e.g., holding a hand rail on bus, and provides efficient mechanical stabilization to upright posture during voluntary movement and external perturbations. Therefore motor programs that involve the hand in a postural role are practiced and are likely to be readily implemented in situations that are expected to result in similar internal perturbations. Jaw muscles, however, cannot generally be used for postural support; therefore it is unlikely that a specific postural set has been established. Given that APAs were immediately apparent in the first repetition of a novel task, we suggest that the CNS uses an intrinsic body map and model of the environment based on current proprioceptive inputs regarding initial conditions to crudely apply postural preparatory programs from familiar conditions to unfamiliar conditions. In this manner, the CNS is able to utilize any body part in contact with a stable support surface to enhance postural stability, and the initial postural adjustment will be based on a strategy derived from a familiar postural support.

FIG. 7. EMG activity in the initial (average of 1st 3 epochs) and peak epochs for each condition and leg lift. ○, ▲, ◊, ◊, initial activity levels; ●, ■, □, ●, peak activity, *, significant difference between conditions. Shaded columns, conditions in which muscles could contribute to stability.
As expected, when a familiar hand support strategy could be used to enhance postural stability, adaptation was rapid. There was no further adjustment of the postural response after the initial repetitions of the HG and HG+BP tasks. The CNS was able to correctly predict the effect of the upcoming internal perturbation and counteract the challenge to stability adequately from the onset of the task. Immediate changes in the postural adjustment were also apparent in the novel bite task; however, the postural response continued to be refined with practice. This lends support to the suggestion that the CNS implements established motor commands and relies on feedback from previous trials to improve subsequent performance (Cordo and Nashner 1982; Nashner 1977).

In addition to the force exerted on the hand grips and bite plate, subjects also leaned against the support. This “lean” strategy adapted with practice for most tasks as evidenced by increased bar force between initial and middle repetitions. A lean strategy is common in everyday situations, e.g., leaning against a wall with your hand is well practiced. However, it is necessary for the CNS to know the potential stability of the structure being leaned against. Thus this component showed gradual adaptation in most conditions, familiar or unfamiliar. Leaning was not generally coupled with the jaw postural strategies, however.

When multiple possibilities for postural support are provided, the entire postural strategy is adjusted.

In conditions with a single support, it was shown that new muscles, specific to the support available, were recruited immediately. The same principle applied to the combined HG+BP condition; however, the relative contribution of muscles at each support was altered compared with its activity in the single support condition. The trunk muscles provide a good example of this. Although the potential for trunk muscles (lumbar erector spinae and obliquus externus abdominus) to contribute to postural stability was not altered by a change in condition, their activity changed when additional support was provided. Jaw muscle activity also changed between the single and multiple support condition even though the ability to participate in postural control was the same. Diastigastic and masseter muscle activity was greater in the single support BP condition and was reduced when the arm muscles could also contribute in the combined HG+BP condition. These results show that the CNS adapts all aspects of the multigroup responses in a multiple support condition rather than simply adding together strategies used in the single support conditions, and this was apparent from the first repetition. The new postural response indicates that the CNS is able to make optimal use of all available support strategies via fine adjustment of the contribution of muscles and shifts in COP, and is able to predict the best possible combination in advance of the task.

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References


