Adaptive changes in anticipatory postural adjustments with novel and familiar postural supports

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Effect of support on APAs

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Abstract

Anticipatory postural adjustments (APAs) serve to stabilise 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 central nervous system (CNS) responded when multiple supports were available. Twelve healthy subjects stood on dual force platforms and performed 20 randomised left and right rapid leg lift tasks in response to a visual cue under 4 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 centre 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 emphasises the flexibility of the CNS to organise postural strategies to meet the demands of postural stability in both familiar and novel situations.
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 central nervous system (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 which 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 hypothesise 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 optimise 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 McIlroy (1997) showed that APAs, determined from changes in centre 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 optimise postural stability in voluntary movements. We hypothesised that conditions which 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 hypothesised 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)
(mean (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, 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 (±3G, sensitivity 360 mV/G, Dimension Engineering, USA) 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 (Fz) of the lower limbs were recorded using two force plates (Bertec Corporation, model 4060-70-4000). Force plate and acceleration data were sampled at 2000 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 diameter target zone. Hand and jaw forces were recorded using custom-made strain gauge hand grips (grip width 64 mm, range 20kg, sensitivity 2.25mV/V, CCT Transducers, Italy) and bite plates (occlusal distance 15 mm, gauge resistance 120Ω, strain range 4%, RS Components, Australia) mounted to a support frame. A force transducer (range 250lb, sensitivity 3.00 mV/V, Scale Components, Australia) 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 leant 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 diameter Ag/AgCl discs, inter-electrode distance 20 mm, Noraxon, USA) were placed over the obliquus 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 L3 spinous process. Electrodes were also placed over the muscle bellies of the biceps brachii (BicB), triceps brachii (TricB), long finger flexors (FingF) and gastrocnemius lateralis (GastL) (Cram et al. 1998).
EMG data were amplified 1000 times, band-pass filtered between 10 and 1500 Hz (Noraxon, USA), and sampled at 2000 Hz using a Power 1401 Data Acquisition System (Cambridge Electronics Design, UK) with Spike2 software and analysed with Matlab 7 (The Mathworks, USA).

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 randomised 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 ~75º 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 three minutes between conditions to minimise 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 analyse as there is no clear distinction between the postural and focal components, 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 analysed 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 (fourth order Butterworth). Similar to gait initiation, the anticipatory postural adjustment (APA) was characterised by an initial medio-lateral shift in centre of pressure (COP) towards the lifted leg followed by a shift towards the stance limb prior to foot off. Thus, the APA was characterised by an increase in vertical force (Fz) 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 Fz increase; peak APA and foot off (Fig. 2). Peak APA was identified as the peak Fz of the lifted leg prior to unloading. Foot off was identified as the point at which Fz 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 2 (repetition 1 and 2), middle 2 (repetition 5 and 6) and last 2 (repetition 9 and 10) repetitions of each leg movement.

EMG data were high-pass filtered at 50 Hz to remove movement artefact (fourth-order Butterworth) and analysed as amplitude in thirty, 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 normalised to peak activity across conditions and averaged over trials. Baseline EMG activity was defined as the average amplitude of the first 3 epochs (60 ms) of each trial (i.e. 340 to 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 analysed 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 Generalised Likelihood Ratio method of onset detection
(Staude 2001). This method has been shown to be superior to onset detection using
standard deviation 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 2, middle 2 and last 2 repetitions to
determine if adaptation occurred.

Statistical Analysis

Statistical analysis was performed using Statistica 7 (Statsoft, USA). Reaction
time, and the onset, amplitude and duration of the anticipatory increase in Fz under the
leg to be lifted were compared between conditions using a repeated measures analysis of
variance (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 Fz under the leg to be lifted and support apparatus
force amplitude and onset) were compared between repetitions (average of first, 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 bite-plate (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 to HG (post hoc: $p = 0.028$) and HG+BP (post hoc: $p = 0.004$). Acceleration did not differ between the HG, BP and HG+BP (post hoc: $p > 0.15$), thus, changes in APA duration and amplitude between the 3 support conditions cannot be explained by changes in leg acceleration.

**Force plate data**

As expected, there was an initial shift of COP towards the lifted limb prior to foot off. Onset of the shift in COP in the US condition, as determined from the increase in Fz under the lifted leg, was initiated 479 (82) ms prior to foot off with an amplitude of 172 (69) N (29% of body weight) and duration of 278 (29) ms.

Amplitude and duration of the anticipatory shift towards the lifted leg (increase in Fz under the lifted foot) were affected by support condition and were smallest and shortest in the condition with maximum support, HG+BP (amplitude 16 (17) N; duration 68 (42) ms), followed by HG, BP and US (Fig. 3). Duration of the anticipatory increase in Fz differed between conditions (main effect: condition $p < 0.001$; post hoc: all $p < 0.007$), and the Fz increase differed between all conditions (main effect: condition: $p < 0.001$, post hoc: $p < 0.001$) except HG+BP and HG (post hoc: $p = 0.36$).
Forces in all four support apparatus increased above baseline levels at least 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 Fz under the leg to be lifted was initiated prior to onset of force in any 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 Fz 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 to 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 to 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 ipsilateral 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 up to 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 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: baseline 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 ms and ~320
ms before foot off, respectively, in the BP condition and ~100 ms 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 $p < 0.001$) (Figure 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, lateralised 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 (Figure 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 $p < 0.001$; post hoc $p > 0.13$). RMS EMG amplitude of OE and LES in right leg lift tasks (muscles ipsilateral to the lifted leg) reached peak amplitude ~20 ms 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 to 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 to 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 stabilisation of the stance limb.

**Adaptation**

The anticipatory increase in Fz under the leg to be lifted showed adaptation by the first repetition of each condition compared to the US control task. Apart from the immediate change in anticipatory increase in Fz, there was no further adaptation in onset of Fz 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 emphasise 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 to 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 Fz), i.e. less movement was required to counteract the destabilising 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 towards 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 stabilise 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 the jaw response contributed to postural support. First, APA duration decreased in the HG+BP compared to the HG condition which suggests the jaw affected anticipatory preparation. Second, 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 stabilisation 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 utilise 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.

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 to 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. Digastric 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 multi-segment 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.
Acknowledgements

This study is supported by the National Health and Research Council of Australia.

We thank Benjamin Powell for his assistance with data analysis.

References


Table 1. *Mean (SD) values for lower limb acceleration and reaction time data*

<table>
<thead>
<tr>
<th>Condition</th>
<th>Lower limb acceleration (ms^-2)</th>
<th>Reaction time (ms)</th>
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<td></td>
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<td>Trigger to foot</td>
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<td>14.0 (5.6)</td>
<td>258 (50)</td>
<td>736 (79)</td>
<td></td>
</tr>
<tr>
<td>Hand grip</td>
<td>11.4 (6.0)</td>
<td>287 (44)</td>
<td>609 (67)</td>
<td></td>
</tr>
<tr>
<td>Bite plate</td>
<td>11.4 (4.6)</td>
<td>273 (43)</td>
<td>752 (117)</td>
<td></td>
</tr>
<tr>
<td>Hand grip + Bite plate</td>
<td>10.4 (6.2)</td>
<td>313 (54)</td>
<td>619 (74)</td>
<td></td>
</tr>
</tbody>
</table>
Figure Legends

Fig. 1. Experimental set-up A. Unsupported B. Hand Grip C. Bite Plate D. Hand Grip + Bite Plate

Fig. 2. Reference points visually identified from vertical ground reaction forces of the lifted limb.

Fig. 3. Mean amplitude and duration of the increase in Fz for each support condition (with 95% confidence intervals). The following conditions are shown: unsupported (US), hand grip (HG), bite plate (BP) and hand grip + bite plate (HG+BP). Of the three support conditions, shift in COP amplitude was greatest in the bite plate condition. There was no difference in amplitude between conditions where the hand was used. Amplitude and duration were greatest in the unsupported condition, however lower limb acceleration was also greater in this condition. NS = not significant.

Fig. 4. Mean onset of changes in background force in support apparatus (bar force, bite plate, left hand grip and right hand grip) and force plate data (Fz) (with 95% confidence intervals). The onset of the increase in Fz occurred prior to onset of forces in other support apparatus, except hand grips in the HG+BP condition. Onset of left and right hand grip forces were always the same within conditions. Bite plate and bar forces were the same in conditions that included jaw support.

Fig. 5. Representative EMG traces, force plate and support force data from one subject in the four experimental conditions. Each trace starts at the time of the visual trigger and time of foot off is indicated by the dotted lines.

Fig. 6. Epoch analysis relative to foot off (dotted line) for rapid lower limb flexion. All epoch data are normalised to peak activity across conditions and displayed with mean and 95% confidence interval for each condition. Closed shapes (square, triangle etc) represent a significant change of EMG activity from baseline levels. A. Right leg lift B. Left leg lift.

Fig. 7. EMG activity in the initial (average of first 3 epochs) and peak epochs for each condition and leg lift. Open shapes indicate initial activity levels, and closed shapes represent peak activity. * = significant difference between conditions. Shaded areas indicate conditions in which muscles could contribute to stability.