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Postural control at the human wrist

John Z. Z. Chew, Simon C. Gandevia and Richard C. Fitzpatrick

Prince of Wales Medical Research Institute and University of New South Wales, Sydney, NSW 2031 Australia

In our movements and posture, we always act against a physical load. A key property of any load is its elastic stiffness (K), which describes how the force required to hold it must change with position. Here we examine how load stiffness affects the ability to maintain a stable posture at the wrist. Loads having positive (like a spring) and negative stiffness (like an inverted pendulum) were created by varying the position of weights on multiarm rigid pendulum. Subjects ($n = 9$) held 15 loads ($K = \pm 0.04, \pm 0.01$ and 0 N m deg^{-1} at mean torques of $0.2, 0.4$ and 0.6 N m) still for 60 s . Residual wrist movement (sway) increased with mean torque and increased as stiffness became more negative. Large effects of load stiffness were seen at low frequencies ($< 1.5 \text{ Hz}$) but not at higher frequencies that reflect load resonance and reflex activity. Subjects accurately perceived their postural sway while holding the loads but measured psychophysical thresholds showed that load stiffness was not perceived. We conclude that load stiffness, independent of force levels, affects the ability to control a load and that the postural control process relies on perception and volitional tracking rather than more automatic reflex pathways. Despite an awareness of their postural errors, we see no evidence for adaptation of postural control processes to compensate for changes in load properties. This is unlike the adaptation of feedforward control processes that produce targeted volitional movements when load properties are altered. We propose that postural control and movement control are fundamentally different neural processes.

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Corresponding author R. C. Fitzpatrick: Prince of Wales Medical Research Institute, Easy Street, Randwick, NSW 2031, Australia. Email: r.fitzpatrick@unsw.edu.au

In all of our actions, we operate on a physical load. We commonly think of these loads in terms of the force required to support them. However, the characteristics of the load, its elastic stiffness, viscosity and inertia, define not only how it will respond to an applied muscular force but also how a muscle behaves for a given level of excitation (Hill, 1964; Partridge, 1966). A load's elastic stiffness describes how the force required to support the load in equilibrium changes with its position. A common experience of elastic stiffness is stretching a spring where the force exerted increases, according to Hooke's law, as the working muscle shortens. A spring-like stiffness we designate as a *positive load stiffness* but load stiffness can be negative in many tasks. Human standing is an example. When we lean forward while standing the calf muscles must generate more force as their anatomical length increases in accord with the physical properties of the body (Fitzpatrick *et al.* 1992).

Since the load properties prescribe unequivocally the force required to maintain a desired posture and the action needed when the limb is displaced from that posture, the brain needs to analyse these constraints on muscle behaviour if it is to control movement and posture. A prevailing view is that this is achieved by the

nervous system establishing an internal forward model of how its actions will move the load and, through inverse dynamic modelling, setting an appropriate regime of centrally driven, feed-forward control, and peripherally driven feedback control (Johansson & Westling, 1988; Neilson *et al.* 1988; Neilson, 1993; Wolpert *et al.* 1995; Fitzpatrick *et al.* 1996; Wing & Lederman, 1998). This control could involve highly automatic reflex mechanisms along with more flexible processes associated with a conscious perception and tracking of the changing posture.

Recent reports by Loram and colleagues (Loram & Lakie, 2002; Loram *et al.* 2005a,b) show that specific patterns of muscular activation are necessary to control standing and that this relates to the large negative-stiffness load of the upright body. As this implies that load properties, other than force, influence the nature of the motor command that is required to control posture, the present work examines the significance of load stiffness for sensorimotor control. We examine postural control at the human wrist, extending the work of Joyce & Rack (1974) to examine the control of loads having negative and positive stiffness and the extent to which postural control is associated with, or relies on, a conscious perception of load stiffness. This

work was presented at the IBRO 2007, Satellite Symposium in Darwin, Australia.

Methods

These experiments were conducted in accordance with the *Declaration of Helsinki* and approved by the institutional Human Research Ethics Committee. Thirteen right-handed adults participated after providing written informed consent. Nine participated in the main postural study and six participated in a study to determine perceptual thresholds for detecting differences in load stiffness.

Experimental design

Load stiffness (K) refers to the linear change in torque (τ) with angle (θ), i.e. $K = d\tau/d\theta$. To hold a positive stiffness load, a person must increase torque if they move to a more flexed joint angle. With negative stiffness loads, less torque is required to hold the load at the more flexed angle. Note here that the external force always acts in the direction of extension and requires a flexion force to maintain the wrist posture. Load stiffness is distinct and independent from the load torque as the same stiffness can exist at different torque levels, and *vice versa*.

A rigid pendulum can be orientated either downward (Fig. 1A) or upward (Fig. 1B) to produce loads of either positive or negative stiffness. For small angle changes (< 10 deg), stiffness is approximately constant. Load torque can be increased or decreased without affecting load stiffness by changing a horizontal counterweight (Fig. 1C). The moment of inertia of the load, which is proportional to the angular acceleration, will also affect torque while there is postural movement. This parameter can be kept constant across loads of different torque and stiffness by adjusting the three weights and their distances from the axis of rotation. A servomotor with torque under feedback control as a linear function of angle can also provide loads of different stiffness and torque (Fig. 1D) that have zero (or negligible) inertial equivalence and can be moved through large angles, neither of which is possible with a real pendulum.

Postural control

Set-up and protocol. Loads of different stiffness were produced by a pendulum comprising three light rigid radial arms mounted in a hub that pivoted on low-friction needle bearings (Fig. 1). Lead weights of different size were clamped at different positions on each arm. Upper and lower arms, 180 deg apart, formed the main axis of the pendulum. Placing most of the mass \times radius on the lower arm created a hanging pendulum with positive load

stiffness (Fig. 1A) whereas placing it on the upper arm created an inverted pendulum with negative load stiffness (Fig. 1B).

At the test position, whether hanging or upright, the pendulum was 10 deg off-vertical and applied an extending force to the wrist, i.e. the subject had to flex the wrist to hold it. The load stiffness (K) at this position is given by:

$$K = \frac{d\tau}{d\theta} = g(m_1d_1 - m_u d_u)\sin\theta$$

where τ is the torque exerted by the pendulum, θ the angle off vertical, m_1 and m_u the masses attached to the lower and upper vertical arms of the pendulum, d_1 and d_u the distance of these masses from the pivot, and g the gravitational constant. At this position, the third arm of the pendulum was set to be horizontal. Weight added to this bar increased the torque offset of the pendulum without changing load stiffness (Fig. 1C). The total torque (τ) required to balance the pendulum complex is given by

$$\tau = gm_h d_h + g(m_1d_1 - m_u d_u)\sin\theta$$

where m_h and d_h are the mass and distance from the pivot for the horizontal arm of the pendulum. The moment of inertia of the pendulum (J) is given by

$$J = \frac{d^2\tau}{d\theta^2} = m_h d_h^2 + m_1 d_1^2 + m_u d_u^2$$

By controlling these masses and distances, we created 15 loads that had identical moments of inertia set to 0.032 kg m² with three levels of mean torque (0.2, 0.4, 0.6 N m) for each of five levels of load stiffness (+0.04, +0.01, 0, -0.01, -0.04 N m deg⁻¹). Fine-tipped needle bearings kept the measured frictional forces to less than 1.3% of mean force. The moment of inertia was accurately controlled (measured $J = 0.032$ kg m², s.d. < 0.002) and did not vary systematically with load stiffness.

Subjects sat with the right arm firmly secured and the hand and wrist joint unencumbered in the flexion-extension plane (Fig. 1E). A long thread attached the hand to a fixation point high above so that subjects did not have to actively support the hand against gravity with a wrist abduction force. They held the pendulum with the wrist 20 deg flexed from the neutral position. The pendulum was 0.7 m away from the hand and held by a light stiff line connecting the back of the hand and the hub of a pendulum. The point of attachment to the hand from the axis of the wrist matched the radius of the hub (80 mm) so that angular excursions of the wrist and pendulum were identical. Subjects, who wore blindfolds, were instructed to hold the load still at the test position for 60 s without 'locking' the wrist by forceful coactivation of the flexor and extensor muscles. The 15 trials were performed in a random order in a single session. A break between trials to change the loads also prevented fatigue.

To examine the effects of load stiffness with minimal inertia, a servomotor replaced the pendulum (Kollmorgen Platinum XT, Danaher Motion, USA). Torque was controlled by PID feedback of a linear function of angle. The moment of inertia of the rotor was 0.0028 kg m^2 (i.e. 8.8% of the real pendulum's moment of inertia), but the feedback control reduced this to an even smaller level at the frequencies of interest (measured estimate from acceleration term = 0.0007 kg m^2). Load stiffness levels tested were ($\pm 0.08, \pm 0.04$ and 0 N m deg^{-1}), a wider

range than was possible with the pendulum. The mean torque level was set at 10% of the subject's maximal voluntary wrist flexion torque (MVC).

Measurement and analysis. Angular position was measured using an optical distance sensor (M27L, MEL Mikroelektronik, Germany) aimed at a reflective target mounted on the pendulum (Fig. 1E) or the servomotor. Torque was measured using a strain gauge that was strapped to the back of the hand, connecting the load

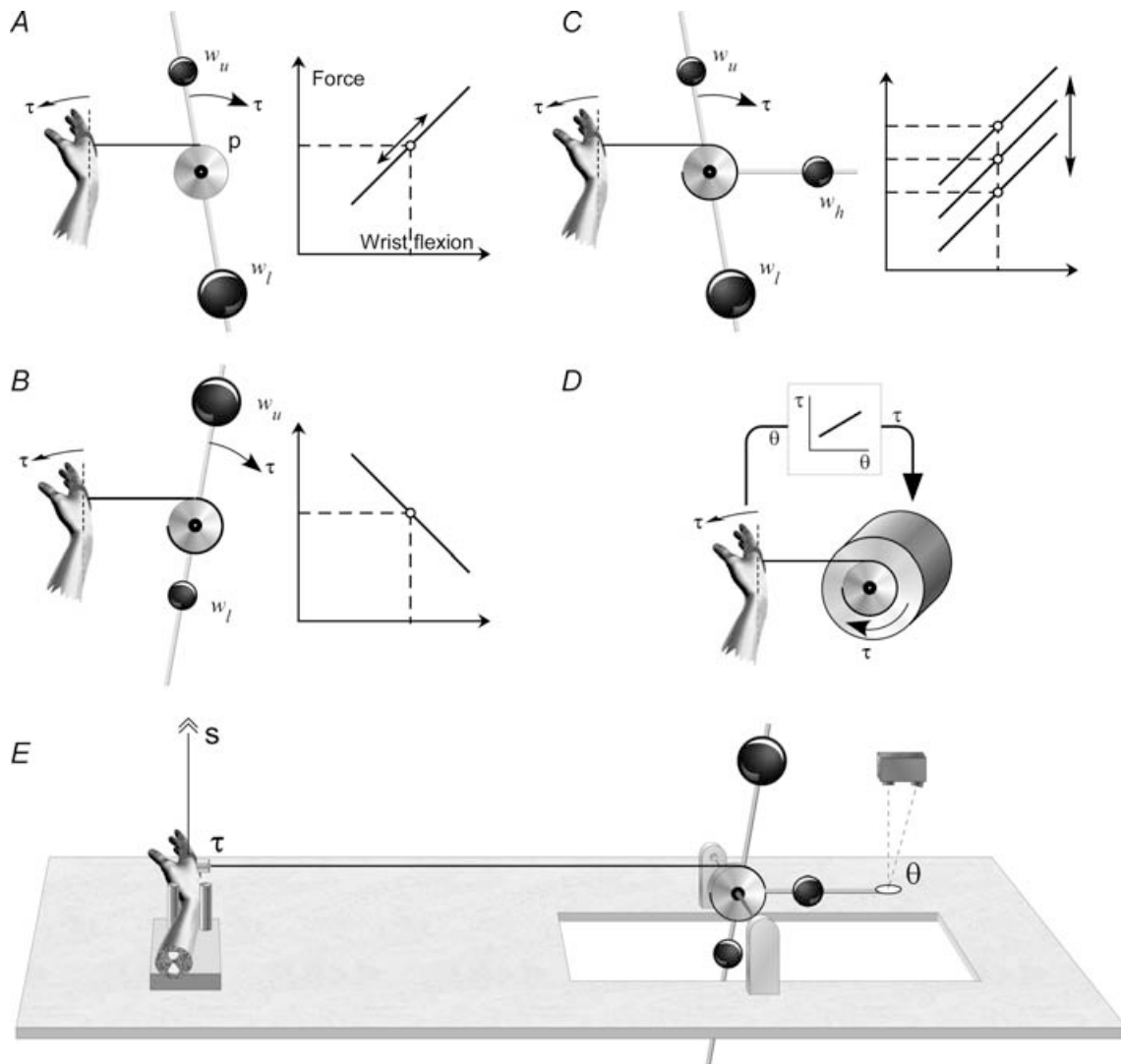


Figure 1. Set-up to produce loads of different stiffness and torque

A rigid pendulum has an elastic stiffness that depends on its orientation. *A*, the hanging pendulum, with greater mass \times length on the bottom arm, is spring-like at small angles. Moving the wrist into flexion requires more force to support the pendulum (positive stiffness). *B*, the same movement made against an inverted pendulum requires less force (negative stiffness). *C*, by adding weight to a horizontal arm, the mean torque can be adjusted without changing the elastic stiffness of the load. *D*, a servomotor tuned under torque feedback as a function of position can approximate these loads. *E*, the set-up of the pendulum experiment shows the forearm restrained with the wrist free to move in flexion/extension only with adduction prevented by a long suspending string (*s*). Torque (τ) was measured with a strain gauge on the back of the hand while movement (θ) was measured with a non-contact laser displacement device.

to the hand. Control tests ensured that the movements recorded at the pendulum and hand were the same. Data were sampled to computer at 2 kHz. Electromyograms (EMG) recorded from Ag–AgCl surface electrodes over flexor carpi radialis and extensor carpi radialis were monitored to ensure that subjects did not coactivate the two muscles while holding the loads.

At the end of each trial, subjects rated the perceived size of their postural movement on a 0–10 visual-analogue scale (VAS: 0 = no movement, 10 = extreme movement). Each subject's VAS score was rescaled to a 0–10 range according to the lowest and highest ratings from the 15 loads.

Analysis of data was performed using Matlab7 software (The MathWorks, Natick, MA, USA). RMS values of wrist angle and torque (4 pole Butterworth 0.25–10 Hz bandpass filtered) were calculated for each trial. Power spectral density functions were calculated with a 0.25 Hz frequency resolution from the unfiltered but detrended angle and torque records. Geometric means were used to average spectra across subjects. Statistical significance of between-condition was determined by ANOVA with subject, torque level and stiffness level as independent factors. Bonferroni's corrections were applied for multiple comparisons with P_α set at 0.05.

Perceptions of load stiffness

The servomotor, controlled as described above, generated the different loads for this study. Subjects were presented with two loads of different stiffness in succession. They 'explored' these loads by making wrist movements that were self-selected in size and velocity. The load having the lower stiffness was designated as the reference load and that with the higher stiffness was designated the test load. They were, however, presented in a randomised order. After 6 s with each load, they reported which of the two was stiffer. The threshold for detecting a difference in stiffness was calculated from the reference stiffness load.

Practice runs familiarized subjects with five reference stiffness levels tested in the study (± 0.08 , ± 0.04 and 0 N m deg^{-1}). The central position of the loads was with the wrist 20 deg flexed from neutral and, at this angle, every load produced the same 10% MVC wrist extending torque. After exploring the first load for 6 s, the stiffness transition to the second load was triggered the next time the wrist passed through the 20 deg point, i.e. the point at which there would be no step in torque. As moving through this point was imperceptible, a sound alerted the subjects of the transition after the 6 s exploration of the first load.

We determined the detection threshold by a method that is frequently used to determine thresholds for detecting joint movements (Sturnieks *et al.* 2006). Subjects were presented with the same reference and test stiffness pair 10 times with the order randomised. In successive blocks of 10, the test stiffness adjusted according to the last correct

detection rate until the target 70% detection level was reached (i.e. subjects correct with 7/10 presentations) or if sequential results went from 8 to 6 (or *vice versa*) in which case the detection level was determined by linear interpolation between the stiffness differences.

Results

Postural control

The forces required to support the loads were relatively small and would not result in any level of fatigue that would affect performance. For the nine subjects tested with the rigid pendulum, the largest wrist torque used (0.6 N m) was equivalent to $4.9 \pm 0.45\%$ MVC (mean \pm s.e.m.). Subjects had little difficulty maintaining the target wrist angle for the duration of a trial. Slow drift over time, which is removed when generating the stationary signal for RMS and spectral analysis, was less than (0.02 deg s^{-1}) for both the rigid pendulum and servomotor loads and was not associated with either the load stiffness level ($F_{4,32} = 0.6$) or mean torque level ($F_{2,16} = 3.4$).

The pattern of residual movement observed when attempting to hold the load still was affected by the load stiffness and mean torque level. For a typical subject, Fig. 2 shows a sample trace of wrist movement for the $+0.04$ and $-0.04 \text{ N m deg}^{-1}$ stiffness levels (left *versus* right) at the 0.2 and 0.6 N m torque levels (top *versus* bottom). Compared with the positive-stiffness load, controlling the negative-stiffness load resulted in a large low-frequency movement superimposed on a similar higher frequency component. The mean level of voluntary torque has a less obvious effect than load stiffness.

Load stiffness and load torque had significant effects on residual postural movement (Fig. 3) and there was no significant interaction between their effects (stiffness: $F_{4,120} = 27.0$, $P < 0.001$; torque: $F_{2,120} = 28.8$, $P < 0.001$; stiffness \times torque: $F_{8,120} = 0.7$). Changing the load stiffness from the most positive to the most negative resulted in a twofold increase in movement amplitude (RMS). This stiffness-related increase in postural movement was nonlinear with an accelerating level of instability across the progression from positive to negative stiffness loads. Non-linear regression of these data, whether exponential, quadratic or hyperbolic, produced significantly better fits than linear regression. Increasing mean torque from 0.2 to 0.4 N m and then 0.4–0.6 N m produced approximately equal increases in movement at each level of load stiffness.

Subjects' perceptions of postural movement while controlling the different loads paralleled actual movement (Fig. 3C). The VAS scores increased with load stiffness ($F_{4,32} = 7.7$, $P < 0.001$) and load torque ($F_{2,16} = 19.6$, $P < 0.001$) as independent factors with no significant interaction ($F_{8,64} = 0.3$).

An almost identical effect of load stiffness was observed with the loads having near-zero inertial equivalent generated by the torque motor (Fig. 3D), with wrist movement increasing in a similar manner when moving from the positive to the negative stiffness loads ($F_{4,24} = 7.0$, $P = 0.001$).

The phase relationship between wrist torque and angle shows that at frequencies below 1.5 Hz, the elastic properties of the load define its response (Fig. 4). Torque and angle are in-phase (0 deg) for positive-stiffness loads and out of phase (180 deg) for negative-stiffness loads. The zero-stiffness load is intermediate but should be viewed with care because of the low coherence between torque and angle (i.e. torque is isotonic at $K = 0$). At frequencies above 2 Hz, torque and angle are out of phase for all loads, indicating that the inertial properties now dominate the response.

Figure 5 displays the averaged angle and torque power spectra for loads of different stiffness and mean torque. One graph for each mean torque level (0.2, 0.4, 0.6 N m) plots the angle spectra (top 3 plots) and the torque spectra (bottom 3 plots) for three levels of load stiffness (-0.04 , 0 , $+0.04$ N m deg $^{-1}$). It is clear that load stiffness and torque have very different effects on postural movement. Whereas the increase in load torque produces a small upward shift of the spectra across the entire bandwidth (compare graphs left to right), the effects of load stiffness are more obvious (compare plots within graphs) and are confined to low frequencies, typically less than 2 Hz. For the negative stiffness load, angle power at these frequencies was approximately an order of magnitude greater than for

the positive stiffness load, with the zero-stiffness load intermediate (e.g. at 0.5 Hz there is a highly significant effect of load stiffness; $F_{4,120} = 11.0$, $P < 0.001$). As expected with an elastic load, the torque spectra reflect both the angle spectra and the load stiffness, i.e. for the negative and positive stiffness loads the torque spectra paralleled the angle spectra but, because torque does not change with angle with the zero stiffness load, power was small at these low frequencies. At higher frequencies the (> 2 Hz) the spectra for different stiffness levels become coincident at any mean torque level (e.g. at 5 Hz there is no significant difference between power at different levels of stiffness; $F_{4,120} = 1.4$). In contrast to this stiffness effect, increasing mean torque at any level of load stiffness increased postural movement and torque uniformly across the entire 0–15 Hz bandwidth.

Above this band of stiffness dependence at the lowest frequencies, a feature of the power spectra is the presence of resonant peaks, which themselves do not respond uniformly to changes in stiffness and mean force. The largest resonant peak, centred at approximately 2 Hz, shows a frequency dependence on load stiffness with lower peak frequencies (ω) for the negative-stiffness loads ($\omega = 2.61 \pm 0.04$ and 1.85 ± 0.04 Hz at $+0.04$ and -0.04 N m deg $^{-1}$, respectively, $F_{4,120} = 52.2$, $P < 0.001$; see bars in Fig. 5) and higher ω with greater mean torque ($F_{2,120} = 15.3$, $P < 0.001$), without a stiffness–torque interaction. This behaviour indicates that this resonance is determined largely by the load properties.

Three smaller resonant peaks that appear at 6, 8 and 10 Hz vary with torque but not stiffness. The 6 Hz and

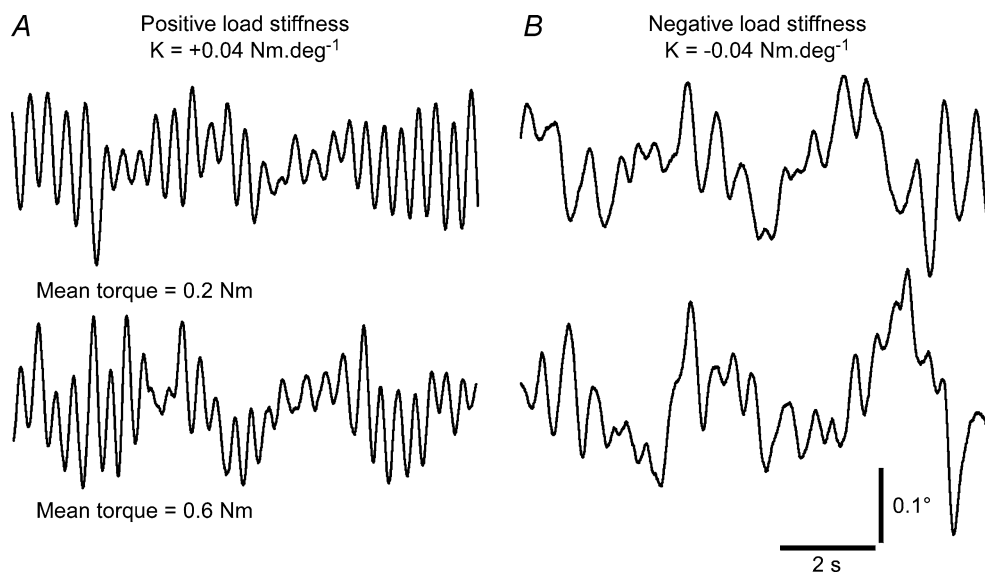


Figure 2. Typical postural records

Wrist movement from a typical subject attempting to maintain wrist position while supporting four different loads ($K = \pm 0.04$ N m deg $^{-1}$ at 0.2 and 0.6 N m mean torque). Loads with negative stiffness (B) result in movement that is markedly different from that with loads of positive stiffness (A) regardless of the mean torque level.

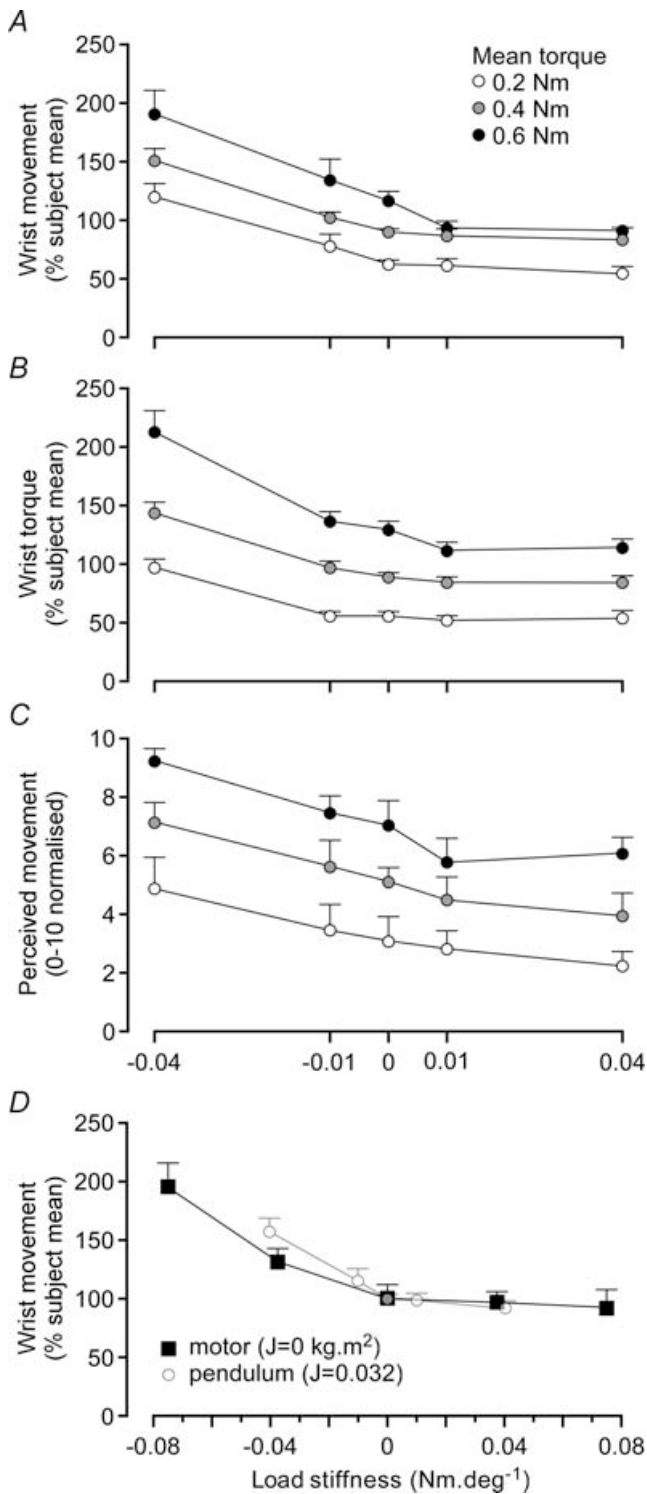


Figure 3. Effects of load force and load stiffness on postural movement

Mean group data of residual wrist movement (A) and torque excursion (B) when holding loads of five different stiffness levels (abscissa) at three mean torque levels. Residual movement was greater while holding loads of negative stiffness than with loads of positive stiffness. C, subjects' perception of movement varied with load stiffness and mean torque, reflecting the size of their actual movement. D, load stiffness had a similar effect on wrist movement for the pure elastic

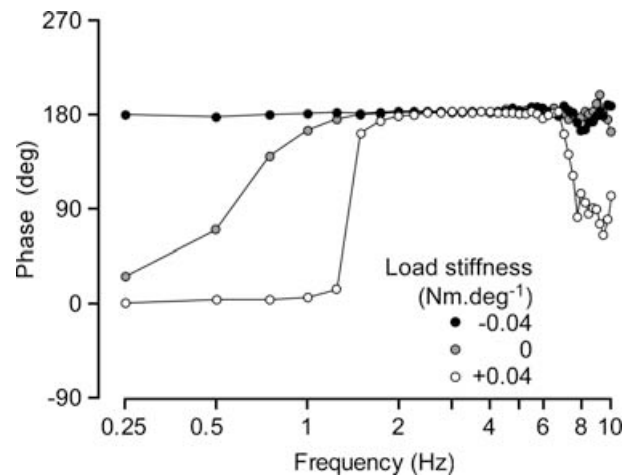


Figure 4. Torque-angle phase for loads of different stiffness

Phase plots between wrist torque and wrist angle for loads of three stiffness levels ($K = +0.04, 0, -0.04 \text{ N m deg}^{-1}$ at 0.4 Nm mean torque; group mean data). The phase transition between 1.5 and 2 Hz indicates a change from dominance of the elastic to the inertial properties of the load.

8 Hz peaks show greater amplitude at lower torque levels whereas the 10 Hz resonance increases with torque. Like the 2 Hz resonance, the principal frequency of the 10 Hz peak increases with load stiffness ($F_{4,111} = 3.9, P < 0.005$) and with mean torque ($F_{2,111} = 8.2, P < 0.001$), whereas the 6 Hz and 8 Hz peaks are unaffected, suggesting that they are based on a different mechanism.

Discriminating stiffness

At the level of reliable (70%) detection of the direction of the change in load stiffness, the difference was $0.058 \pm 0.007 \text{ MVC force per degree}$ (mean \pm s.e.m.) and this was not affected significantly by the reference stiffness level ($F_{4,24} = 0.64$). In absolute units, this equates to $0.021 \pm 0.005 \text{ N m deg}^{-1}$. There appeared to be a nonlinear trend with mean detection values increasing with the absolute value of the reference stiffness (Fig. 6A) although regression of these absolute-value data across all subjects fell short of a statistical significance at our criterion ($R^2 = 0.051, n = 30$).

The angular excursions of wrist movement while making these detections (Fig. 6B), which are the span between the maxima of wrist flexion and extension, were not significantly different across load stiffness levels ($F_{4,500} = 2.27$). In contrast, the torque ranges explored

loads with zero inertia ($J = 0$) generated by the servo-motor. The motor data are plotted with the corresponding pendulum data normalized by subject to the zero-stiffness load. Note that the scale is changed because the motor data were determined for a wider range of load stiffness levels.

(Fig. 6C) varied widely with load stiffness ($F_{4,500} = 310$, $P < 0.001$), being approximately in proportion to the absolute value of the reference stiffness and greater under the stiffer test loads than under the reference ($F_{1,500} = 48.1$, $P < 0.001$).

Linear regression of the torque excursions for the test load against those of the reference load across all subjects (Fig. 6D) revealed a highly linear relationship ($R^2 = 0.95$). The torque range was $13.6 \pm 3.0\%$ greater for the stiffer test loads compared with the reference. As this is consistent with Weber's rule of just noticeable differences, it appears that subjects detected the difference in stiffness by making movements of equal magnitude and judging the difference in torque.

Discussion

When we hold a posture, we operate on a physical load. It may be just a limb or the body but it often involves an additional external load, as we have studied here. These experiments show that our ability to control posture depends very strongly on the elastic stiffness of the load being held. Thus, the central motor control process cannot adapt in a way that allows the same precision of postural control for different loads.

In the absence of external perturbations, the movement error seen when we attempt to hold a chosen posture reflects the sensorimotor control process. Sources of this error may arise through inaccurate sensory detection of movement, through noise generated within the CNS, and finally through limits on the constancy of force output

from muscles. Here we must consider the meanings of 'noise' and 'error' with caution and accept that they are likely to be integral to the control processes of the brain (Stein *et al.* 2005).

Load force and posture

Postural movement increased approximately in proportion with the mean force level required to hold the load. This effect of force could, in part, result from the pattern of muscle recruitment during voluntary contractions (Milner-Brown *et al.* 1973). In accord with the size principle (Henneman, 1957), unfused force output from progressively larger motor units creates fluctuations in force and movement in proportion to the force level (Jones *et al.* 2002). The 10 Hz peak in the spectra (Fig. 4) is likely to be the result of a resonance produced by the injection of this muscle dynamic into the control loop as it increases with mean force level and has a frequency consistent with the recruitment firing rate of motor units in a human arm muscle (Denier van der Gon *et al.* 1985). Stochastic discharge of the motor neurons on a longer time scale also results in a force-dependent motor noise at lower frequencies (Jones *et al.* 2002; Bays & Wolpert, 2007).

On the sensory side of the control process, the effect of force level is less clear. The available psychophysical studies of proprioceptive acuity give different, although not necessarily conflicting, answers. Proprioceptive performance is reported to improve with low-level muscle contraction (Gandevia & McCloskey, 1976; Taylor &

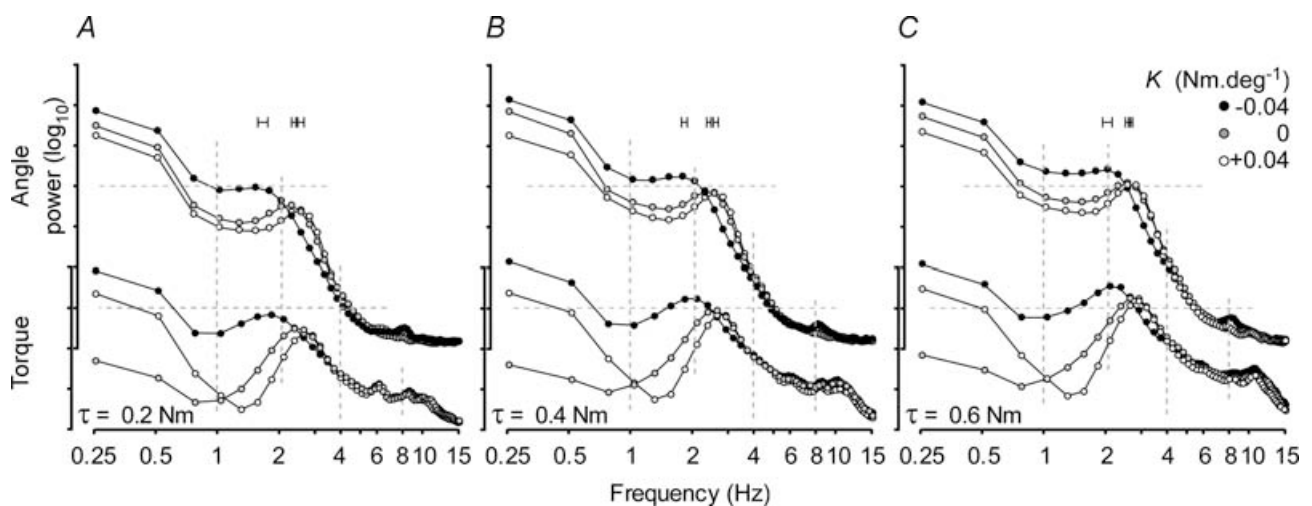


Figure 5. Power spectra of wrist torque and angle for different loads

Group mean power spectra ($n = 9$) of wrist torque (lower 3 plots) and angle (upper 3 plots), with each set normalized by each subject's mean power across the 15 loads tested. The three spectra for different load stiffness levels ($+0.04$, 0 , -0.04 N m deg $^{-1}$) are grouped by mean force into the three graphs (A, 0.2; B, 0.4; C, 0.6 N m). The gridlines are for reference. Three regions of the spectra can be distinguished. Below 1.5 Hz, power varies widely with load stiffness, being least for the positive stiffness and most for the negative stiffness loads. Between 1.5 Hz and 3 Hz are large resonant peaks with stiffness-dependent differences in their peak frequencies (group ranges are shown by the bars above). Above 4 Hz there appear smaller resonant peaks at 6, 8 and 10 Hz.

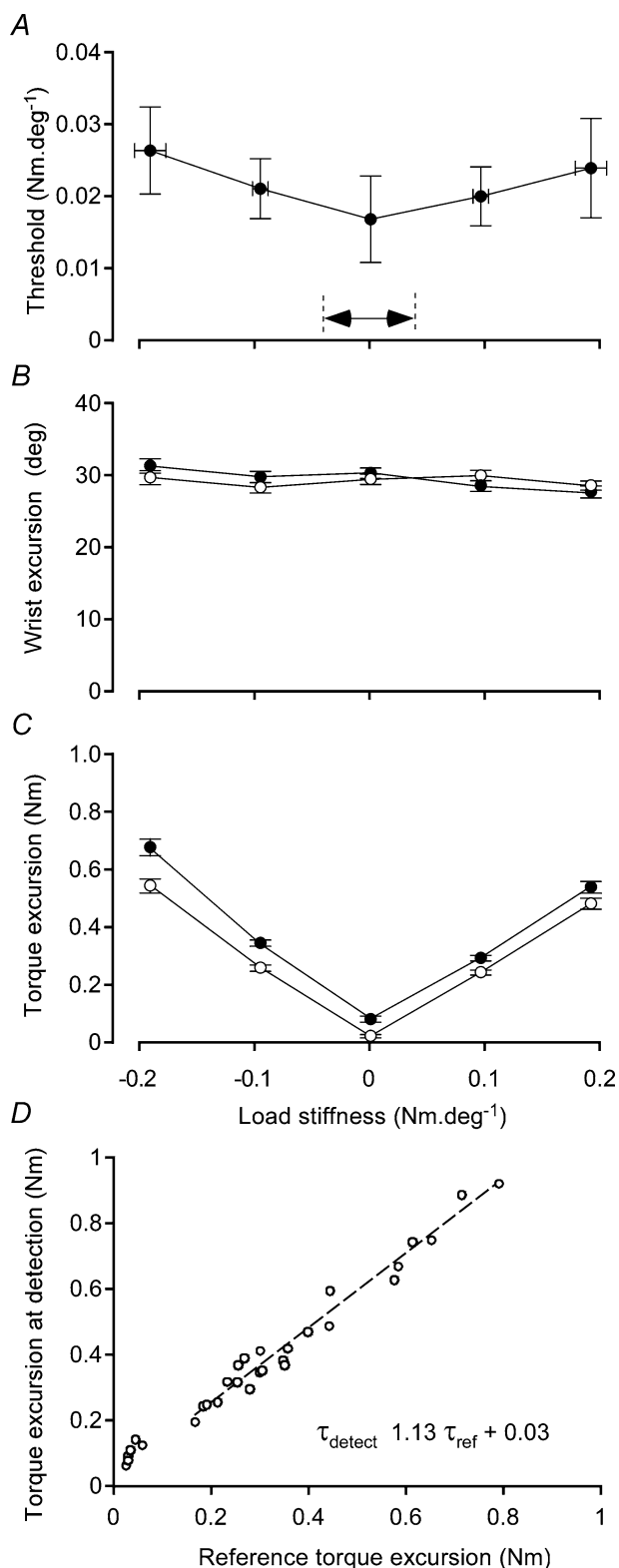


Figure 6. Stiffness perception

A, difference in load stiffness required for 70% correct detection ($n = 6$, mean \pm s.e.m.) are not significantly different across 5 reference stiffness levels. B, at the detection threshold, subjects moved the wrist through excursions of approximately 30 deg across the range of load stiffness levels tested. C, with these movements, the torque excursion

McCloskey, 1992) but at higher forces it may worsen (Wise *et al.* 1998). At the force levels tested in these studies, we believe that we are operating at the low end of this range and we are not seeing effects of a gross deterioration in sensitivity for movement detection, a view supported by the observation that subjects could reliably report the actual size of their postural movement across the different force levels (Fig. 3D).

Load stiffness and posture

The effect of load stiffness on posture was independent of the level of force required to hold the load. This is shown by statistical independence in predicting the total amount of postural movement (Fig. 3) and by the different frequency bandwidths at which stiffness and force affect postural movement (Fig. 4). Increasing load force increased postural movement across the entire frequency domain (0.25–15 Hz). In contrast, the effect of load stiffness was very large at frequencies below approximately 1.5 Hz (Fig. 5) whereas it had no effect at higher frequencies (> 4 Hz). This behaviour suggests the involvement of two different control processes, one operating at lower frequencies that compensates for changes in load stiffness and one operating at higher frequencies that adapts poorly to changes in load stiffness.

Tonic stretch reflexes at the human wrist respond most effectively to small-amplitude (~ 0.3 deg) movements at frequencies above 4 Hz (Cathers *et al.* 1999). Thus, reflex activity could explain the equalization of high-frequency postural movement across the different levels of load stiffness. However, it is not possible to see in these closed-loop observations whether reflex transmission is tuned to deal with load stiffness. Indeed, at these frequencies, elastic stiffness may not be a concern to the nervous system as the response of this wrist load, and probably any real-world load, will be dominated by inertial rather than elastic properties (Fig. 4).

The frequency of the most prominent resonance (ω) is centred around 2 Hz. If we model the system as a simple closed-loop harmonic oscillator (like an undamped spring or pendulum), the squared resonant frequency (ω^2) is estimated by the sum of all elastic stiffness components divided by the mass of all moving components of the system. Since only systems with net positive stiffness can resonate and we see resonance for

explored varied greatly with the reference stiffness. Open circles are the reference loads, filled circles the test loads. D, for each subject and load stiffness, the torque excursion explored for the test load is plotted against that for the reference load. The Weber fraction for detecting the stimulus difference (0.13) is obtained from the regression slope. The very low reference stiffness values (grey) are excluded from the regression estimate of the Weber fraction.

loads of negative stiffness, the total stiffness of the muscle, passive elements, and the neural feedback loop must have a magnitude greater than the load's. This resonant frequency increases with mean force (consistent with an increase in intrinsic muscle and tendon stiffness) and decreases when moving from positive to negative stiffness (Fig. 5). Closer inspection suggests that the stiffness provided by the other active component, neural feedback, remains relatively constant across load stiffness (i.e. ω^2 increases monotonically with load stiffness at each force level). This suggests a relatively constant neural feedback gain across the different stiffness levels. The extent to which neural feedback control actually contributes is debatable. Studies in which external perturbations are applied suggest a large reflex contribution (Joyce *et al.* 1974) but the gain of the tonic stretch reflex is low at these frequencies, amplitudes and force levels (Cathers *et al.* 1999, 2004). In many situations, this load-dependent resonance will occur at much lower frequencies (e.g. the standing body or even an outstretched arm). We have selected to study these particular loads at the wrist to separate this resonance from the postural movement that occurs at very low frequencies, the control of which we discuss here.

At the lowest frequencies (< 1.5 Hz) the elastic properties of the load dominate, as revealed by the phase relationships between wrist torque and angle (Fig. 4). It is here that the major effect of load stiffness is seen, and the reasons for this are likely to be complex. Because a compliant tendon links the contractile element of the muscle to the load with nonlinear progression between short- and long-range stiffness (Loram *et al.* 2005a; Loram *et al.* 2007), the control of muscle length must vary dramatically across load of different stiffness and force. If load stiffness becomes sufficiently negative, an intermittent or pulsatile motor output becomes obligatory (Lakie *et al.* 2003). Regardless of the causes, it is clear that any adaptation of the control process operating at these frequencies poorly compensates for changes in load stiffness.

The control process at these low frequencies appears to be associated with a conscious perception of movement and some level of volitional response as subjects have an accurate perceptual awareness of the changes in postural movement across different stiffness levels (Fig. 3D). The response bandwidth for human voluntary tracking of kinaesthetic stimuli at the elbow is restricted to frequencies below 2 Hz (Neilson, 1972; Cathers *et al.* 1996), supporting the view that this control involves high-level volitional activity.

Load stiffness is not perceived during postural control

When subjects were asked to report which was the stiffer of two presented loads, they could detect at threshold a difference of approximately $0.02 \text{ N m deg}^{-1}$ (Fig. 6). Here,

we examined the $K = 0$ condition and just a small fraction (2%) of the stiffness range covered by Jones & Hunter (1990) in their report of stiffness perception at the elbow. Therefore, we consider this to be an absolute threshold for stiffness detection rather than a just noticeable difference that follows Weber's rule. In judging stiffness, subjects chose to make movements of a standard size (~ 30 deg) and judge the difference in the torque range explored. The Weber fraction determined from these torque ratios was 0.13, which is at the upper end of previous reports for discriminating force (Ross & Brodie, 1987; Jones, 1989). Stiffness thresholds appear to reflect limitations in force perception.

To reach the threshold for perception of load stiffness, subjects made large volitional angle and torque excursions of the wrist (i.e. ~ 30 deg and $\sim 0.1 \text{ N m}$; Fig. 6). However, postural movement was just a small fraction (< 4%) of these levels while the loads were held still. Looking at the traces in Fig. 2, typical angular excursions were of the order of 0.2–0.3 deg, and this would equate to mere 2–3% changes in force level. Considering that the best reported detection levels for force are of the order of 10% (Ross & Brodie, 1987; Jones, 1989), it would appear that there is no information available to the nervous system to provide for a perception of load stiffness while a steady posture is maintained. We can conclude that it is unlikely that subjects have perceptual access to load stiffness while maintaining a steady posture. A similar phenomenon can be experienced in other postural tasks. When standing still, we can be aware of the torque exerted by the feet on the ground but we are unaware of the very high negative stiffness of the load being balanced unless we voluntarily make much larger body sways.

On controlling posture and movement

Maintaining 'posture' refers to the process of keeping one part of the body stationary with respect to another. Holding the wrist still, as studied here, and holding the body still when standing are both examples of postural control. The functional feedback control that is the major determinant of postural stability operates at a high volitional level and is associated with a clear perception of postural movement. For several reasons, we consider that volitional tracking is the principal process by which the stable posture is maintained. It is now well recognized that postural control, albeit during standing, requires cognitive resources and is adversely affected by simultaneous tasks requiring cognitive activity (Kerr *et al.* 1985; Maylor *et al.* 2001). By controlling load stiffness independently from other factors, we have shown that the low-frequency bandwidth at which load stiffness affects postural control coincides with the bandwidth of voluntary tracking and that subjects have an accurate perception of the size of their postural movement. Highly automatic reflex activity

appears to be less important in determining postural performance with these natural unperturbed loads.

There is evidence that the nervous system simulates internally the dynamics of its motor output to plan, execute and learn patterns of motor output that will achieve a desired outcome (Wolpert *et al.* 1995; Scott, 2004). The response and resulting sensory feedback is predicted from the central motor command. In conjunction with an inverse dynamic model, muscle forces are calculated to generate a motor command that will achieve the desired outcome, optimizing performance by taking into account noise in the system. Feed-forward control improves after repeated exposure (Weeks *et al.* 1996; Lackner & DiZio, 2002) unless access to afferent feedback is disrupted so that performance errors are not perceived (e.g. Cole & Sedgwick, 1992; Vercher *et al.* 2003).

The proposed existence of such forward internal models is based on a relatively precise adaptation in generating large and purposeful targeted movements when the load conditions or target are changed (Wolpert *et al.* 1995; Lackner & Dizio, 1998). In contrast, we see no evidence that the postural control process adapts to deal with changes in load properties in a way that compensates for them – despite the awareness of the movement errors while maintaining the wrist posture with different load conditions. In other words, the limits of the adaptation to different loads for postural control do not parallel those seen for large purposeful movements; the former is relatively poor, the latter quite precise.

For movement, cognitive awareness of load properties or limb mechanics in addition to feedback of performance error might be integral to creating the forward control model. However, during postural control, movements are very small and, although subjects can perceive these movements, they cannot perceive the changes in load properties responsible for the large differences in postural performance. It may be significant that feed-forward control of movement does not adapt if afferent feedback is disrupted (e.g. Cole & Sedgwick, 1992; Vercher *et al.* 2003). During postural control, the residual movement is small and approaches the perceptual limit while the afferent force signal appears to be subliminal. This may represent an equivalent disruption of sensory feedback that prevents adaptation of feed-forward control.

From these results we propose that postural control and movement control are different and may involve fundamentally different neural processes. Strong evidence for a difference is seen in the responses of individual neurons in the primary motor cortex of monkeys during posture and movement tasks; one-quarter of neurons responding to load are active only during the postural task, one-quarter during the movement task and the rest switch their responses between tasks (Kurtzer *et al.* 2005; see also Scott, 2007). There are two interesting implications here. The first is that for postural control, performance limits

may be set by peripheral sensorimotor factors, whereas for movement control, performance limits may arise through control processes within the central nervous system. The second implication is that these concepts are at odds with models such as equilibrium-point control (e.g. Feldman, 1986; Bizzi *et al.* 1992a,b) in which a unified continuum linking movement and posture has been envisaged.

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John Z. Z. Chew, Simon C. Gandevia and Richard C. Fitzpatrick

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