Mobility as the purpose of postural control

Charlotte Le Mouel[1*], Romain Brette[1]

[1]Sorbonne Universités, Université Pierre et Marie Curie (UPMC) Univ Paris 06, INSERM, CNRS, Institut de la Vision, 75012 Paris, France

*** Correspondence:**
Corresponding Author
charlotte.le-mouel@inserm.fr

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Abstract

Counteracting the destabilizing force of gravity is usually considered to be the purpose of postural control. However, from the consideration of the mechanical requirements for movement, we argue that posture is adjusted in view of providing impetus for movement. Thus, we show that the posture that is usually adopted in quiet standing in fact allows torque for potential movement. Moreover, when performing a movement - either voluntarily or in response to an external perturbation - we show that the postural adjustments are organized both spatially and temporally so as to provide the required torque for the movement. Thus, when movement is performed skillfully, the force of gravity is not counteracted but actually used to provide impetus to movement. This ability to move one's weight so as to exploit the torque of gravity seems crucial, especially for recovering one's balance when a standing person is perturbed by an external force.

1 Introduction

The purpose of postural control is usually considered to be to counteract the destabilising force of gravity, be it in quiet standing, reactions to perturbations by external forces, or in voluntary movement (Bouisset and Do, 2008; Horak, 2006; Massion et al., 2004; Nashner et al., 1989). Physiological and biomechanical analyses of posture therefore focus on the stability of the centre of mass (CoM). Stability can be understood in a variety of ways (Hasan, 2005), but the one that is most commonly used for understanding posture is that stability implies that any deviation of the CoM from its equilibrium position is opposed and corrected, such that the CoM is returned to its equilibrium position. As argued by Hasan (2005), this notion stems from an analysis of how linear systems respond to perturbations: in linear systems, if deviations from the equilibrium position are not corrected, then they grow exponentially. It is therefore assumed that if postural adjustments cannot or do not correct for deviations in the position of the CoM, then the person will inevitably fall. Balance (the ability to prevent falling) is therefore thought to require immobilising the CoM (Bouisset and Do, 2008; Horak, 2006; Massion et al., 2004; Nashner et al., 1989). From this assumption, it follows that moving poses a threat to balance, since any voluntary movement might displace the CoM. Such a perturbation must be corrected for by a postural adjustment whose purpose is to immobilise the CoM. This has led to the conceptual distinction between muscles considered as "prime movers", responsible for the movement, and muscles considered as "stabilisers", responsible for the immobility of the CoM despite movement. Thus, when someone performs a movement of the upper

body, such as leaning forwards, the "prime movers" are considered to be muscles of the upper body. Their contraction is preceded and accompanied by the contraction of muscles in the lower leg (Cordo and Nashner, 1982; Lee et al., 1990; Pedotti et al., 1989). Their action is thought to immobilise the CoM despite movement.

However, our analysis of the mechanical requirements for moving shows that the action of the lower leg muscles is to provide impetus for movement. Indeed, impetus can only be provided by the external forces, which, when standing on the ground, only consist of the ground reaction force and one's own weight. We will argue that postural control consists in inducing impetus for movement, both from the ground reaction force, through the contraction of the muscles of the body segments directly in contact with the support, and from one's own weight, through the control of the position of the CoM.

In the first part, we will show that in quiet standing there is a range of CoM positions which can be stabilised by the postural control system, and the position at which the CoM is actually maintained can be understood in view of providing impetus for potential movement. In the second part, we will show that the postural adjustments which precede and accompany well-practised movements do not serve to immobilise the CoM but actually displace it so that one's own weight can be exploited to provide impetus for movement. Thus, postural control only immobilises the CoM during quiet standing but not during movement. We therefore propose that the purpose of postural control is not to immobilise the CoM, but to provide impetus for movement.

2 The standing posture enables movement

In quiet standing, people maintain their CoM relatively immobile, vertically aligned with the middle of their feet. How is this posture maintained and why is it adopted?

2.1 Mechanical requirements for balance

In order for someone to stand still in a given position, the sum of the external forces and of their torques must be zero. We will show that there is a range of standing postures in which this requirement may be satisfied.

2.1.1 Torques of the external forces

When someone is standing on the ground, there are two external forces exerted on them: the person's weight and the ground reaction force.

Gravity exerts a downwards vertical force whose magnitude is the person's weight (their mass times the gravity of Earth). The point of application of the person's weight is called the centre of mass and noted CoM. If the CoM is vertically aligned with the ankles, then the person's weight does not exert a torque around the ankles (Fig. 1A). If it is forwards of the ankles, then the weight exerts a forwards torque which is equal to the weight times the horizontal distance between the CoM and the ankles (Fig. 1B).

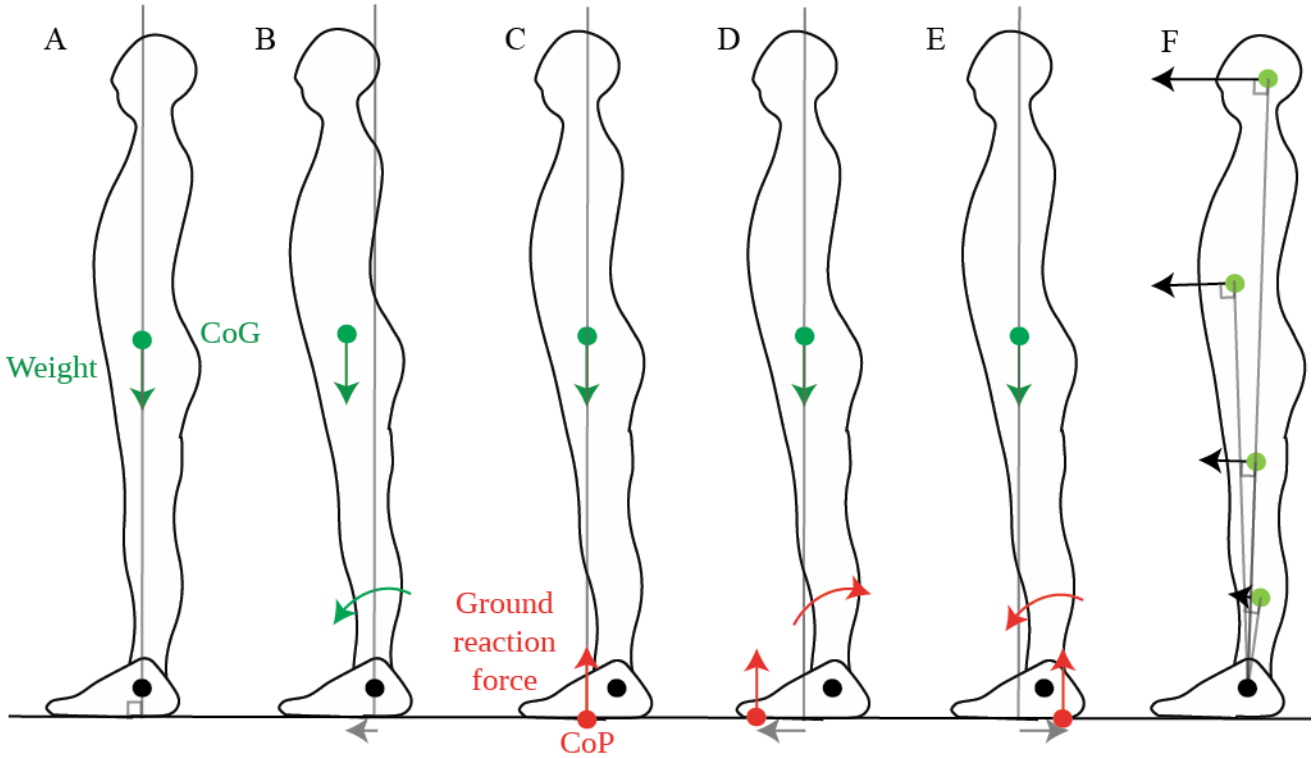


Fig. 1 Torques of the external forces and rotational momentum of the body.

A. When the CoM (green dot) is vertically aligned with the ankle joint (black dot), the weight (green arrow) exerts no torque around the ankle. B. The torque exerted by the weight around the ankle is proportional to the horizontal distance between the CoM and the ankle. C. When the CoP (red dot) is vertically aligned with the CoM, there is no net torque, since the torque around the ankles of the ground reaction force (red arrow) is the opposite of the torque of weight. D. When the CoP is forwards of the CoM, there is net backwards torque around the ankle. E. When the CoP is backwards of the CoM, there is net forwards torque around the ankle. F. The person's rotational momentum around their ankles is the sum over the body segments (represented by green dots) of the segment's mass times its distance to the ankle (grey line) times its rotational speed, i.e., its speed perpendicularly to the axis joining it to the ankle (black arrow, perpendicular to the grey line).

The ground supports the person's weight, therefore, as long as the CoM remains at the same height, the vertical component of the ground reaction force is of equal magnitude but of opposite direction to the person's weight. The ground reaction torque is therefore equal to the weight times the horizontal distance between the ankles and the point of application of the ground reaction force, called the centre of pressure and noted CoP.

The net torque around the ankles is thus determined by the horizontal distance between the CoP and the CoM: if they are vertically aligned, there is no net torque (Fig. 1C), if the CoP is forwards of the

CoM, then there is a net backwards torque (Fig. 1D), and if the CoP is backwards of the CoM, then there is a net forwards torque around the ankles (Fig. 1E).

Such torque induces a change in the person's rotational momentum around their ankles, which is the sum over their body segments of the segment's mass, times its distance to the ankle, times its rotational speed (its speed perpendicularly to the axis joining it and the ankle), as represented in Figure 1F.

2.1.2 Immobilization of the CoM during quiet standing

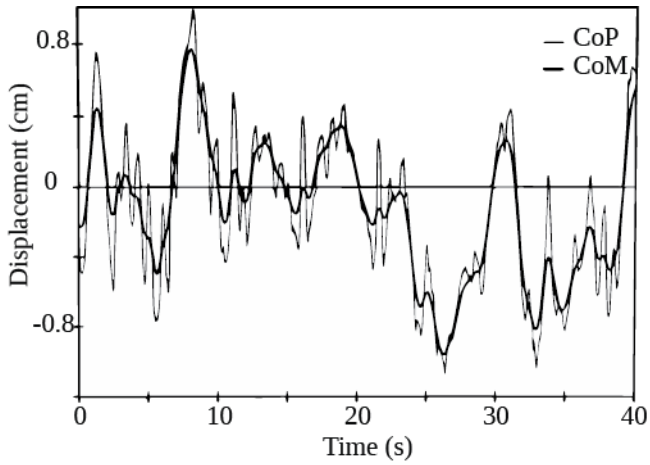
What are the mechanical requirements for stabilizing the CoM at a given position in quiet standing? As long as the person remains straight, immobilizing the CoM is equivalent to maintaining the rotational momentum at zero. The torques of the external must therefore cancel out: the mean position of the CoP must be vertically aligned with the mean position of the CoM. Moreover, whenever the CoM moves forwards of the CoP, there is a net forwards torque exerted on the person by the external forces, which accelerates the CoM forwards. In order to return the CoM back to its mean position, it must be accelerated backwards. This requires net backwards torque, and therefore requires the CoP to move forwards of the CoM. Indeed, when the positions of the CoP and CoM are recorded in a person standing quietly, it is observed that the CoM and CoP do not remain immobile, but that there are small ongoing shifts in the CoM which are tracked with a few milliseconds delay by the CoP which overshoots the CoM (see Fig. 2, adapted from Winter et al., 1998). This allows the person to maintain their CoM within a narrow range, typically less than a centimeter.

2.1.3 CoM position during quiet standing

When no instructions are given, the mean position of the CoM is vertically aligned with the middle of the foot, a few centimetres forwards of the ankle joint, such that the person leans forwards by a few degrees. However, when requested to do so, a young person can maintain their CoM at positions up to 40 % of their foot length forwards of its typical position, and up to 20 % backwards, without this providing a challenge to balance (Schieppati et al., 1994). The amplitude of the CoP shifts used to maintain the CoM at a given point are typically less than a centimetre, which is an order of magnitude smaller than the range of CoM positions that can be maintained. In quiet standing, the position of the CoM can therefore be stabilised over a wide range.

Fig. 2 Correlated CoP and CoM shifts

Displacement of the CoP and CoM in quiet standing as a function of time, adapted from Winter et al. (1998): small ongoing shifts of the CoM are tracked and overtaken by shifts in the CoP (with a few milliseconds delay that cannot be seen in this figure).



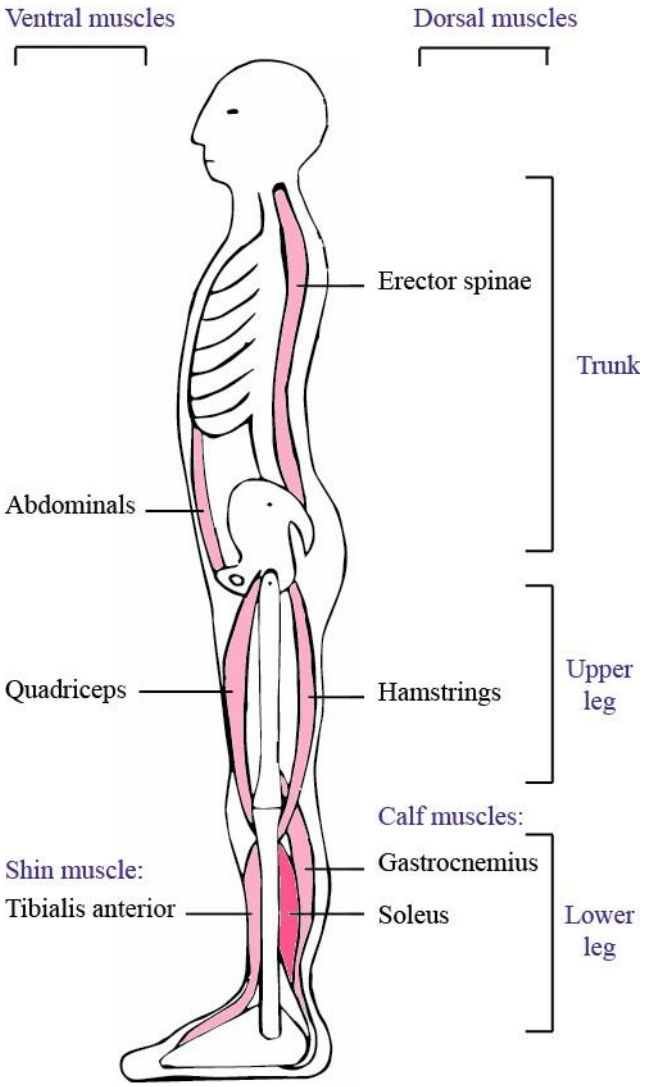


Fig. 3 Anatomy

Schematic representation of the muscles and their attachment points; classical muscle denominations are in black, the denominations used in the text are in blue.

If the position at which the CoM is actually stabilised stemmed from the requirement not to fall, then when this requirement is made more stringent, such as when someone stands facing the edge of the platform they are standing on (making it all the more important not to fall forwards), the CoM should be shifted as far backwards as possible. In this situation, the CoM is indeed shifted backwards, but by less than a centimetre (Carpenter et al., 2001), which is an order of magnitude smaller than the backwards CoM shift than can be maintained without posing a threat to balance.

Why then would the position of the CoM be tightly controlled to remain vertically aligned with the middle of the foot, if this is not a requirement for balance? We will argue that the position of the CoM in quiet standing is controlled in view of providing torque for potential movement.

2.2 Mechanical opportunities for movement

What are the mechanical requirements for movement? When a standing person wants to perform a movement such as leaning forwards (while keeping their feet immobile on the ground), this requires a transient increase in the person's forwards rotational momentum around their ankles. Only the

torques of the external forces may affect the person's rotational momentum. Muscular contraction can therefore only produce torque for movement by inducing a change in the ground reaction torque or in the torque of gravity. We will show that changes in muscular contraction can induce an immediate change in the ground reaction torque but not in the torque of gravity. Figure 3 is a schematic representation of the muscles we will refer to as well as their attachment points, and presents the denominations we will use in the text.

2.2.1 Lower leg muscle contraction changes the ground reaction torque

We will show that only the forces exerted by the lower leg muscles onto the foot may change the ground reaction torque around the ankles.

In order to understand how the internal forces induced by muscular contraction may affect the ground reaction force, we shall decompose the body and consider only the foot (Fig. 4). If the foot is on a rigid support and does not slip, then it can neither translate, nor rotate around the ankle. Therefore, both the sum of forces and the sum of torques around the ankle must be zero. The forces exerted onto the foot are the ground reaction force (see the red arrow in Fig. 4), the foot's weight (which is negligible compared to the other forces), and the forces exerted by the lower leg onto the foot through on the one hand the muscles which attach onto the foot (see the blue arrows in Fig. 4), and on the other hand the bones, which exerts no torque around the ankles since it is applied at the ankles (see the green arrow in Fig. 4).

Thus, as long as the ground prevents the foot from moving, the torque of the ground reaction force around the ankle is exactly the opposite of that of the muscles of the lower leg. When the calf muscles contract, this pulls the heel upwards through the Achilles tendon (Fig. 4A). If the foot were in the air, it would rotate around the ankle joint bringing the toes down. Since the foot is against rigid ground, the ground resists the rotation of the foot by exerting backwards torque on the foot. Thus, any increase in the force that the calf muscles exert on the heel is instantly translated into an increase in the backwards torque of the ground reaction force on the entire body. As we have seen, as long as the CoM remains at the same height, the vertical component of the ground reaction force is of equal magnitude but of opposite direction to the person's weight. Since the magnitude of the vertical component of the ground force does not change, contraction of the calf muscles can only induce backwards ground reaction torque by shifting the CoP forwards (Fig. 4A right panel). Likewise, any increase in the force of the shin muscle is instantly translated into an increase in the forwards torque of the ground reaction force on the entire body, through a backwards shift in the CoP (Fig. 4B).

2.2.2 The ground reaction torque is limited by the extent of the foot

However, the CoP cannot move further forwards than the toes. Thus if the contraction of the calf muscle exerts a torque that is larger than the product of the person's weight and the distance between their ankle and toes, then the foot can no longer remain immobile: the foot must then rotate around the toes. Indeed, when subjects are asked to rise onto their toes, they perform this movement with a burst of contraction of their calf muscles (Nardone and Schieppati, 1988) (Fig. 4C). Likewise, shin muscle contraction induces forwards ground reaction torque by shifting the CoP backwards.

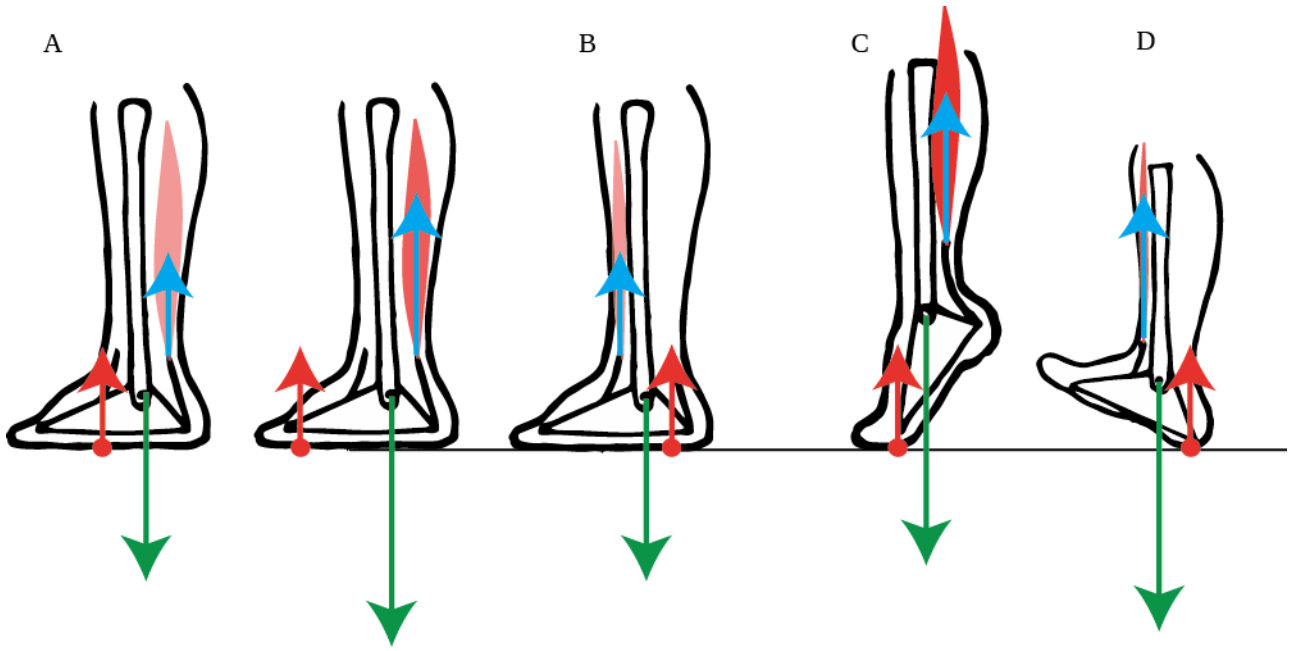


Fig. 4 Torques exerted on the foot

A-C: The force exerted by the lower leg bones onto the foot (green arrow) exerts no torque around the ankle. The torque of the ground reaction force (red arrow) and of the forces exerted by the lower leg muscles onto the foot (blue arrow) are therefore opposite when the foot remains immobile: A. the torque around the ankles exerted by the calf muscles onto the foot is instantly compensated for by a forwards shift of the CoP (red dot). B. The torque around the ankles exerted by the shin muscle onto the foot is instantly compensated for by a backwards shift of the CoP. C. When the backwards torque exerted by the calf muscles is too large, the person rises onto their toes. D. When the forwards torque exerted by the shin muscle is too large, the person rocks onto their heels.

However, the CoP cannot move further backwards than the heel. Thus when subjects are asked to rock onto their heels, they perform this movement with a burst of contraction of their shin muscle (Fig. 4D) (Nardone and Schieppati, 1988).

The potential ground reaction torque is therefore limited by the extent of the foot: the forwards torque is limited to the product of the person’s weight and the distance between the heels and the ankles, and the backwards torque is limited to the product of the person's weight and the distance between the ankles and toes.

2.2.3 The net torque is limited by the position of the CoM

The ground reaction torque changes instantly when the torques exerted by the lower leg muscles on the foot change, but it is limited by the extent of the foot. The torque of weight on the other hand can only be changed by displacing the CoM forwards or backwards, which cannot be done instantly but first requires the sum of the external forces to accelerate the CoM horizontally. Therefore, at a given instant, the potential net torque that can be induced by muscular contraction is limited by the position of the CoM: the net forwards torque is limited to the product of the weight and the distance between

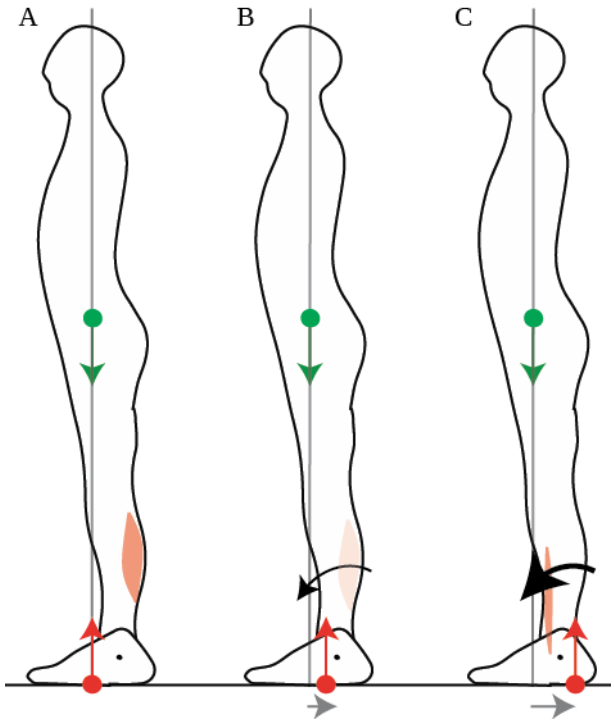


Fig. 5 Forwards leaning

A. In normal quiet standing, tonic calf muscle contraction maintains the CoP (red dot) forwards of the ankles, vertically aligned with the CoM (green dot). B. A decrease in tonic calf muscle contraction causes the CoP to shift backwards towards the ankle, resulting in small net forwards torque around the ankles. C. Silencing the calf muscles and contracting the shin muscles causes the CoP to shift backwards of the ankle towards the heel, resulting in large net forwards torque around the ankles.

the CoM and the heels, whereas the net backwards torque is limited to the product of the weight and the distance between the CoM and the toes.

In order to produce at short notice movements which require either forwards or backwards torque, the CoM should therefore be maintained near the middle of the foot.

2.3 How the standing posture is adapted for potential movement

We therefore suggest that the position of the CoM in quiet standing is tightly controlled to remain within less than a centimetre of the middle of the foot, not as part of a requirement for balance, but as part of a requirement for movement. We will now show how muscular contraction patterns adjust the standing posture in view of movement.

2.3.1 Tonic contraction of the calf muscles

If the CoM were maintained vertically aligned with the ankle, then the weight would exert no torque around the ankles, therefore the standing posture could be maintained without tonic contraction of either the calf muscles or the shin muscle. However, the net forwards torque that could be induced by shin muscle contraction would then be limited to the product of the weight and the horizontal distance between the heel and the ankle. In turn this would limit the speed of movements requiring forwards rotational momentum. Instead, in the normal standing posture, the CoM is maintained forwards of the ankles, near the middle of the feet (Fig. 5A) (Sasagawa et al., 2009). This requires tonic calf muscle contraction so as to compensate for the forwards torque of weight.

If a movement involving forwards rotational momentum need then be produced, forwards torque can be contributed not only by the contraction of the shin muscle, but also by a decrease in the contraction of the calf muscles. Thus, when someone is asked to lean forwards (Crenna et al., 1987), if this movement is performed slowly, then it requires little net forwards torque and can be performed merely by decreasing the tonic activation of the calf muscles. This shifts the CoP backwards towards the ankle joint, resulting in small net forwards torque (Fig. 5B). If the movement is performed rapidly, then the tonic calf muscle activity is silenced, which brings the CoP below the ankle joint, and then the shin muscle contracts, which brings the CoP backwards of the ankle towards the heel (Fig. 5C), resulting in large forwards torque.

Thus, maintaining the CoM in the middle of the foot allows for both net forwards and backwards torque to be induced by changes in the contraction of the lower leg muscles.

2.3.2 Standing on a slope

This position of the CoM is maintained even when this requires a change in the tonic contraction, such as when standing on a slope (Fig. 6A (Sasagawa et al., 2009)). This implies that the force exerted by the calf muscles on the heel must also be also constant. The calf muscles have a mechanical stiffness such that, for a given level of contraction, the force they exert is stronger when they are stretched. Thus, for a given level of contraction, the force exerted by the calf muscle would increase when going from a slope with the toes down, to a flat slope, to a slope with the toes up. This would not allow the CoM to be maintained at a constant position despite changes in slope. Instead, what is observed is that the contraction of the calf muscles adapts to the slope, and decreases when going from a slope with the toes down (Fig. 6A left panel), to a flat slope (Fig. 6A middle panel), to a slope with the toes up (Fig. 6A right panel), such that the CoM remains above the middle of the foot (Fig. 6A) (Sasagawa et al., 2009).

2.3.3 Handstands

Another suggestion that the position of the CoM is controlled in view of potential movement rather than in view of immobility comes from acrobats performing handstands. Clément and Rézette (1985) observed acrobats at various competitive levels performing handstands. All the acrobats were able to maintain their balance in the upside-down posture, however they did so in different ways. The acrobats at lower competitive levels maintained their mean CoP a few millimetres forwards of their wrist; they could therefore maintain their posture with very little tonic contraction in the arm muscles (Fig. 6B, left). The acrobats at higher competitive levels maintained their mean CoP more forwards of their wrists, with the acrobat at the highest level maintaining his mean CoP 3 cm forwards of his wrists; this posture requires tonic contraction of the wrist extensors (Fig. 6B, right). Since all the acrobats were capable of maintaining their balance upside down, but had attained different competitive levels, we suggest that maintaining the CoM in the middle of the hands improves not only the capacity for balance but more crucially the capacity for movement.

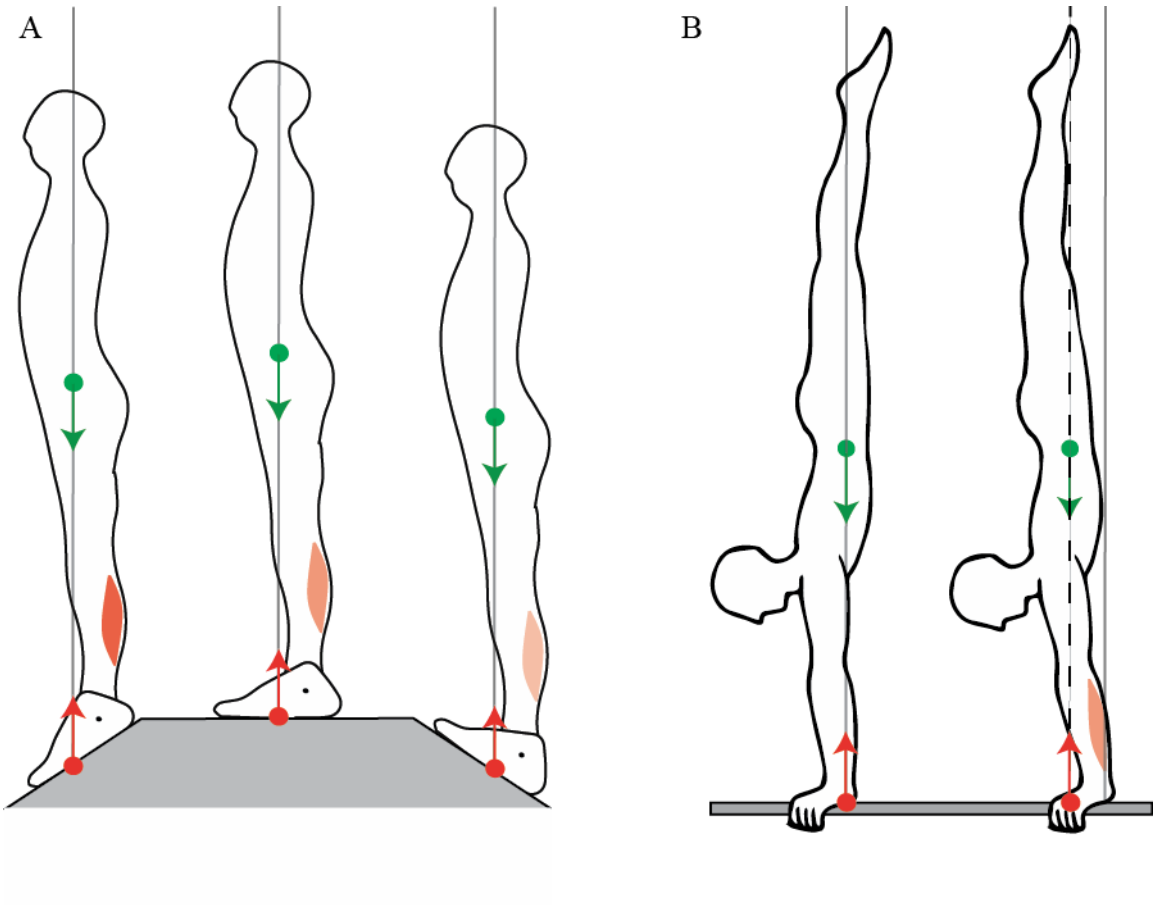


Fig. 6 Adaptation of the position of the CoM

A. The tonic calf muscle contraction decreases when going from a slope with the toes down (left panel), to a flat slope (middle panel), to a slope with the toes up (right panel) such that position of the CoM is maintained vertically aligned with the middle of the feet. B. Left panel: Acrobats at lower competitive levels maintain their CoP and CoM aligned with their wrist without tonic contraction of their wrist extensors. Right panel: Acrobats at higher competitive levels maintain their CoP and CoM forwards of their wrist, through tonic contraction of their wrist extensors.

2.4 Summary

The mechanical requirements for stabilising the position of the CoM in quiet standing can be met in a wide range of postures. We therefore suggest that in quiet stance, the position of the CoM is maintained vertically aligned the middle of the feet, not because such a posture is necessary for balance, but because such a posture allows for both forwards and backwards torque to potentially be induced by changes in the contraction of the lower leg muscles.

3 Postural adjustments enable movement rather than immobility

We have shown that the position of the CoM is controlled in view of potential movement. We will now argue that when a movement is performed, postural control does not serve to immobilize the CoM, but on the contrary adjust the position of the CoM so as to provide impetus for movement.

3.1 Postural adjustments in voluntary movement

When someone performs a movement of the upper body which requires rotational momentum, the contraction of the upper body muscles is accompanied, and often preceded, by the contraction of muscles of the lower legs (Cordo and Nashner, 1982; Lee et al., 1990; Pedotti et al., 1989).The assumption that the purpose of postural control is to immobilise the CoM despite movement leads to the conceptual distinction between the muscles of the upper body as “prime movers”, and the muscles of the lower legs as “stabilisers”(Massion et al., 2004). According to our hypothesis however, the purpose of postural control is not to immobilise the CoM but to provide torque for movement. In this view, the contraction of the lower leg muscles should be considered integral to the movement itself, since it immediately induces ground reaction torque, any may also serve to accelerate the CoM so as to induce torque from weight.

3.1.1 Pulling on a handle

When someone pulls on a handle placed in front of them, the contraction of the arm muscles is preceded then accompanied by the contraction of the calf muscles (Cordo and Nashner, 1982; Lee et al., 1990).

The contraction of the calf muscles throughout the duration of the contraction of the arm muscles can be understood as stabilising the position of the CoM, as suggested by Cordo and Nashner (1982). Indeed, when pulling on a handle, the handle reaction force exerts forwards torque on the person around the ankles, equal to the product of the force and the height of the handle (Fig. 7A). For the person to be able to pull on the handle without falling forwards, the sum of torques of the external forces around the ankles must remain zero. The contraction of the calf muscles induces backwards ground reaction torque which counteracts the forwards reaction torque of the handle (Fig. 7A).

However, the initial contraction of the calf muscles, before the contraction of the arm muscles, cannot be understood as stabilising the position of the CoM. On the contrary it accelerates the CoM backwards (Fig. 7B). This is consistent with our hypothesis, in that backwards acceleration of the CoM increases the backwards torque of weight throughout the movement. In turn, this allows for larger force to be exerted on the handle (Fig. 7C). Indeed, when the person is asked to pull harder on the handle, then this initial period lasts longer, the calf muscle activation is stronger, and the initial backwards acceleration of the CoM is larger (Lee et al., 1990). Thus, postural adjustments during handle pulls do not allow for the CoM to be immobilised. On the contrary, they are temporally organised so as to provide torque for movement, both from the ground reaction force and from the person’s weight.

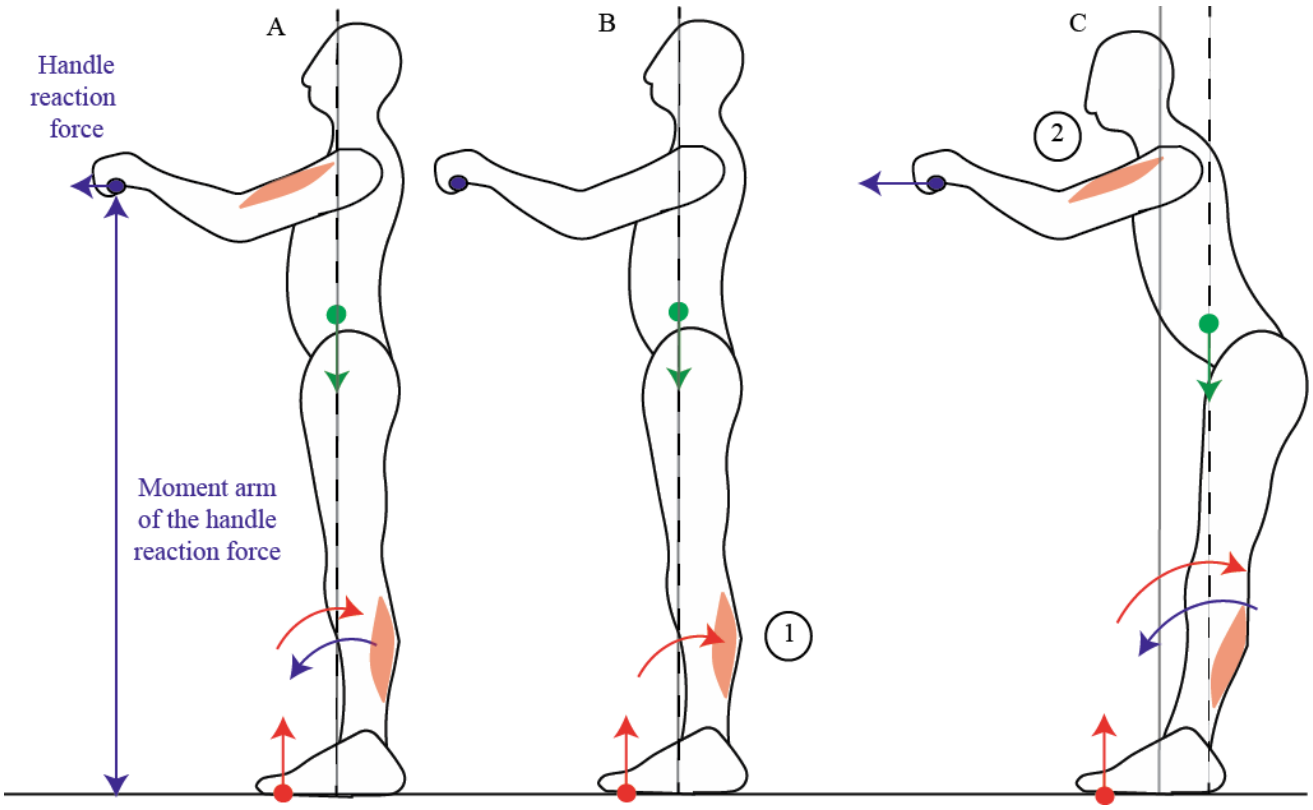


Fig. 7 Pulling on a handle

When pulling on a handle, the handle reaction force (blue arrow) exerts forwards torque around the ankles which can compensated for by contracting the calf muscles (A). In preparation for pulling on a handle, subjects contract their calf muscles before their arm muscles (B), which displaces their CoM backwards, allowing for a larger net backwards torque to be exerted during the handle pull (C).

3.1.2 Leaning the trunk

When someone leans the trunk backwards fast, the contraction of the dorsal trunk muscles is accompanied by the contraction of the calf muscles (Crenna et al., 1987).

The contraction of the calf muscles throughout the duration of the contraction of the dorsal trunk muscles can be understood as stabilising the position of the CoM, as suggested by (Crenna et al., 1987). Indeed, if only the dorsal trunk muscles contract, then the trunk rotates backwards around the hips (Fig. 8A). However, this backwards acceleration of the mass of the trunk implies that the trunk pushes forwards on the hips, which are therefore accelerated forwards. Since only the lower leg muscles may influence the ground reaction torque, contraction of the dorsal muscles does not induce a change in the person's rotational momentum around their ankles. The increase in backwards rotational momentum around the ankles due to the backwards acceleration of the head must therefore be compensated by an equal increase in forwards rotational momentum due to the forwards acceleration of the hips. Since the head is further from the ankles than the hips are, and since rotational momentum is proportional to distance, this implies that the forwards acceleration of the hips exceeds the backwards acceleration of the head, such that the CoM is accelerated forwards.

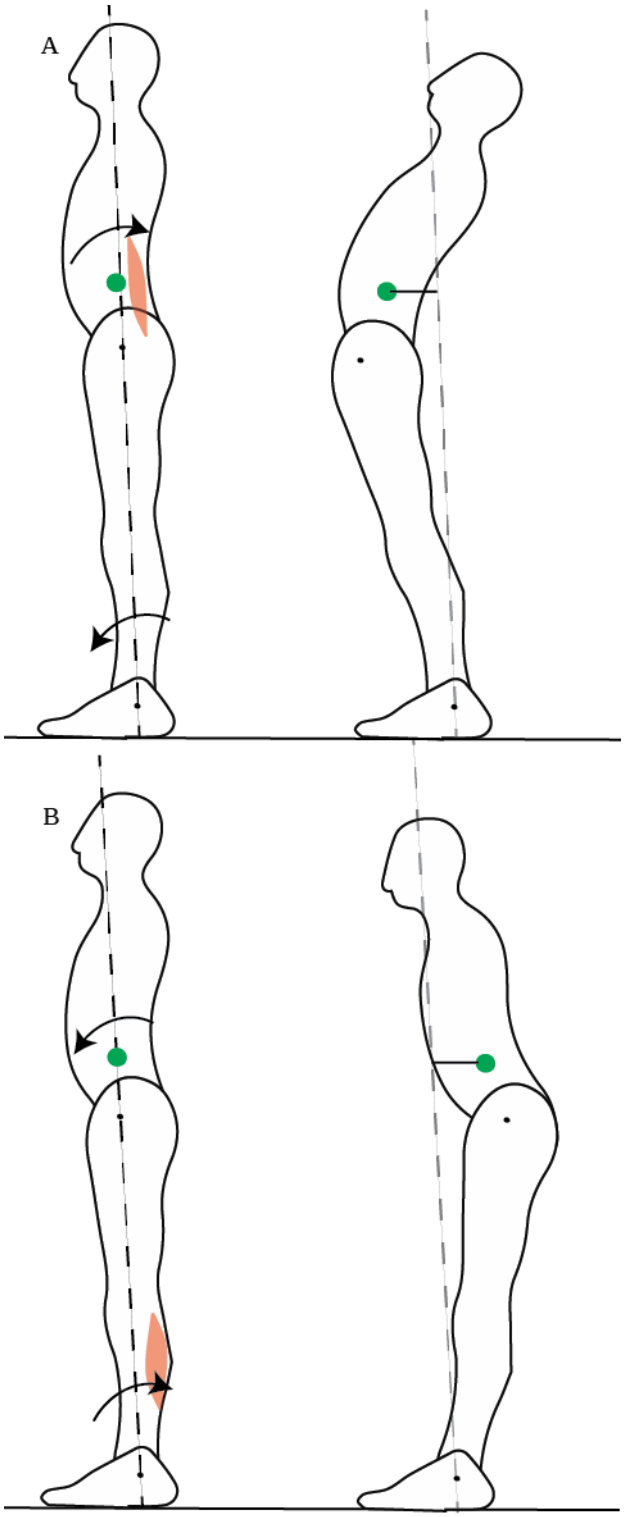


Fig. 8 CoM acceleration induced by muscular contraction

A. Dorsal trunk muscle contraction makes the trunk rotate backwards around the hips while the legs rotate forwards around the ankles, accelerating the CoM forwards. B. Calf muscle contraction makes the legs rotate backwards around the ankles while the trunk rotates forward around the hips, accelerating the CoM backwards.

Thus, contracting only the dorsal trunk muscles accelerates the CoM forwards (Fig. 8A). Contracting the calf muscles accelerates the CoM backwards (Fig. 8B), such that combining the two may allow for the CoM to be immobilised, as suggested by (Alexandrov et al., 2001).

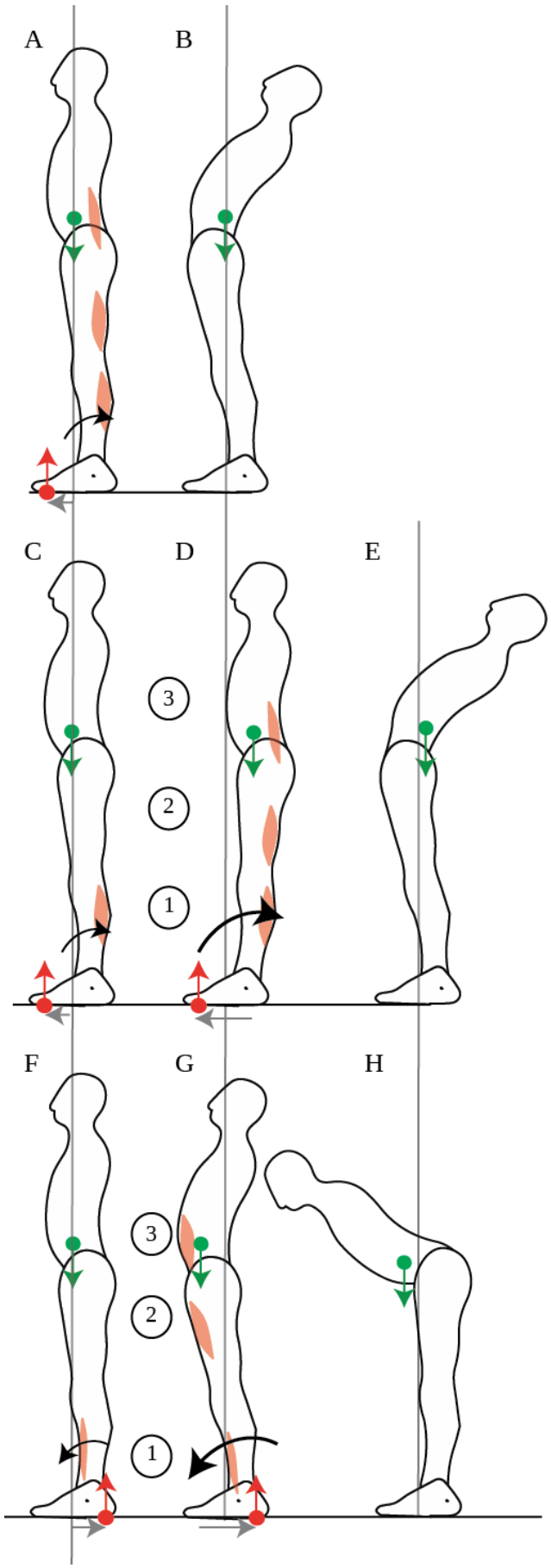


Fig. 9 Fast leaning of the trunk

When control subjects perform fast backwards leaning, the dorsal muscles contract simultaneously (A), which increases backwards rotational momentum without translating the CoM (B). When gymnasts perform fast backwards leaning, the initial contraction of the calf muscles (C) accelerates the CoM backwards, thus allowing for more net backwards torque during the subsequent contraction of the dorsal muscles (D) which enables the gymnast to lean the trunk (E). When leaning forwards fast, the initial contraction of the shin muscle (F) accelerates the CoM forwards, thus allowing for more net forwards torque during the subsequent contraction of the ventral muscles (G), which enables the person to lean the trunk (H). The sequence of activation of the muscles is indicated by the numbers 1 to 3.

This prediction is however in contradiction with the observation that, when the movement is well practised, the contraction of the calf muscles does not immobilise the CoM, but on the contrary is temporally organized so as to initially accelerate the CoM in the direction required for the movement (Pedotti et al., 1989). Thus whereas control subjects perform fast trunk bending through simultaneous contraction of their calf and dorsal trunk muscles (Fig. 9A-B), when gymnasts perform this movement (for which they presumably have more practice than controls), the concurrent contraction of the dorsal muscles is preceded by the contraction of the calf muscles alone (Fig. 9C-E).

This initial contraction of the calf muscles is a direct prediction of our hypothesis: since the maximal backwards torque around the ankles is limited by the distance between the CoM and the toes, initially accelerating the CoM backwards through the contraction of the calf muscles allows for the movement to be performed faster. Indeed, gymnasts can lean their trunk backwards faster than control subjects (Pedotti et al., 1989).

This temporal sequencing of the onset of muscular contraction is moreover found even in control subjects when they are asked to lean forwards fast (Crenna et al., 1987), a movement for which they presumably have more practice than leaning backwards. There is thus initially a silencing of the tonically active calf muscles. After a short pause, the shin muscle contraction starts (Fig. 9F), followed by the contraction of the abdominals (Fig. 9G). The CoM is thus initially accelerated forwards, such that forwards trunk bending (Fig. 9H) is performed twice as fast as backwards trunk bending.

Further evidence that the purpose of the initial contraction of the lower leg muscles is to increase the net torque around the ankles comes from the experiment performed by Oddsson and Thorstensson (1987). They asked people to perform forwards leaning movements of different amplitudes. Small movements require less torque, and in this case the abdominals contract before the shin muscle. As the amplitude of the movement increases, the shin muscle is contracted earlier and earlier until its contraction precedes that of the abdominals for the largest trunk movements.

We therefore suggest that, when leaning the trunk, the trunk and lower leg muscles do not play the opposite roles of “prime mover” and “stabiliser”, but rather play the same role of providing torque for movement. Indeed, leaning the trunk requires not only an increase in the trunk’s rotational momentum around the hips, through the contraction of the trunk muscles, but also an increase in the person’s total rotational momentum around the ankles, through the contraction of the lower leg muscles.

If we take into account the knee joint, then the same analysis shows that leaning the trunk also requires the contraction of the thigh muscles, and that efficient trunk leaning should be performed by contracting first the lower leg, then the thigh and finally the trunk muscles. Indeed, whereas in control subjects lean the trunk backwards, the calf, dorsal thigh and dorsal trunk muscles are recruited synchronously (Fig. 9A), in gymnasts the calf muscles are recruited first, followed by the dorsal thigh and then the dorsal trunk muscles (Fig. 9D) (Pedotti et al., 1989). Likewise, when leaning forwards, the shin muscle contracts first, followed by the ventral thigh muscles then the abdominals (Fig. 9G)(Crenna et al., 1987).

Postural adjustments occurring before and during voluntary movement should therefore be interpreted as providing torque for movement, rather than immobilising the CoM. Indeed, the temporal organisation of muscular contraction patterns actually initially accelerates the CoM in the direction which increases the net torque for movement.

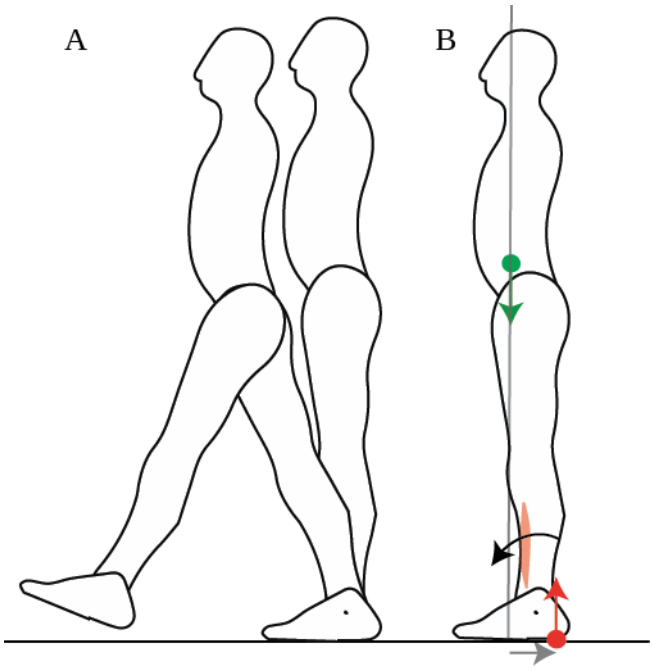


Fig. 10 Gait initiation

A. Gait initiation requires an increase in forwards rotational momentum around the ankle of the stance leg (black dot). B. Forwards torque is provided by the silencing of the calf muscles and the contraction of the shin muscle, which shifts the CoP backwards towards the heels.

3.1.3 Gait initiation

This initial acceleration of the CoM at the onset of movement is crucial when a standing person starts to walk. When taking a step, the trunk advances forwards, the stance leg rotates forwards around the ankle, and the swing leg swings forward (Fig. 10A). For a standing person to take a step therefore requires an increase in forwards rotational momentum around the ankle of the stance leg. Forwards torque may be provided by shifting the CoP backwards, and further increased by accelerating the CoM forwards. Indeed, when a standing adult starts walking, the calf muscles are silenced and the shin muscles contract, such that the CoP shifts backwards (Fig. 10B), and the CoM is accelerated forwards before the swing foot is lifted from the ground (Burleigh et al., 1994). The faster the person is asked to walk, the larger this initial backwards shift in the CoP (Brenière et al., 1987). Moreover, when children learn to walk, there is a gradual increase in this forwards acceleration of the CoM which allows them to walk faster (Bril et al., 2015; Ledebt et al., 1998). Thus, this anticipatory adjustment does not immobilize the CoM despite movement, but on the contrary provides thrust for walking by accelerating the CoM forwards.

3.2 Postural reactions to perturbations

Thus, whereas postural control immobilizes the CoM in quiet standing, when a well-practiced voluntary movement is performed, the CoM is no longer immobilized. On the contrary postural adjustments initially accelerate the CoM so as to exploit the torque of one's own weight for moving. We will now argue that when the standing posture is perturbed by an external force, balancing reactions which prevent falling actually rely on this capacity to move the CoM.

A standard experimental paradigm to perturb the standing posture is to have the person stand on a platform which is then translated. For example, if a person stands quietly on a platform which is then translated backwards, then the person finds themselves leaning forwards (Fig. 11 A), with their CoM no longer aligned with the middle of the feet. Two responses are commonly observed: the person

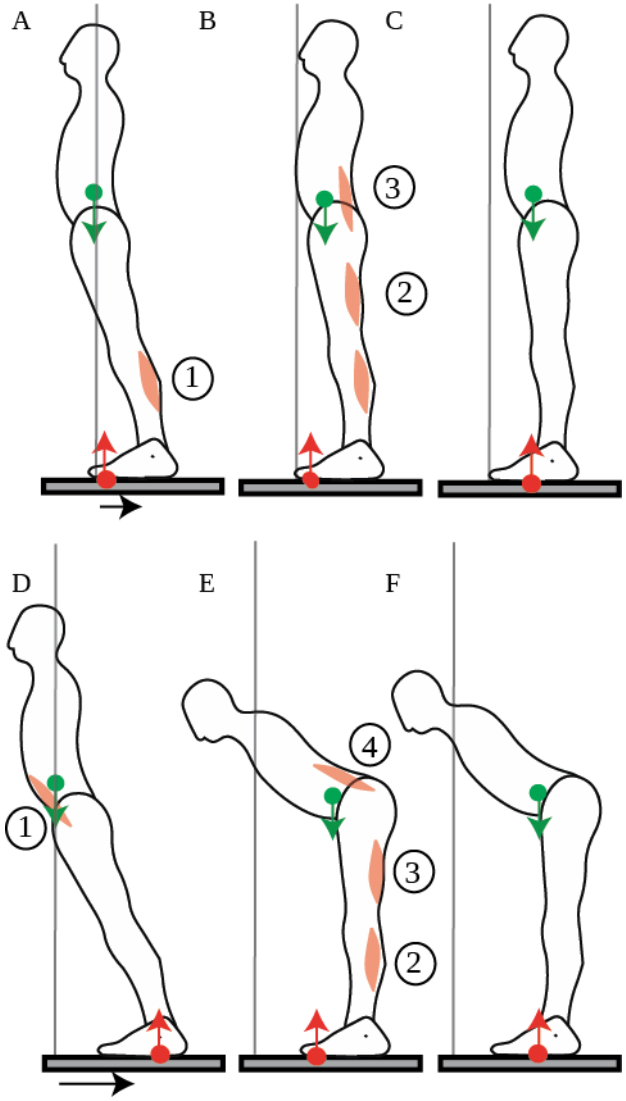


Fig. 11 Platform translation

A-C: After a slow platform translation (black arrow), the initial contraction of the calf muscles (A) accelerates the CoM backwards, allowing for more net backwards torque during the simultaneous contraction of the dorsal muscles (B), which enables the person to rotate around their ankles (C). D-F: After a fast platform translation (black arrow), the initial contraction of the abdominals (D) accelerates the CoM backwards, allowing for more net backwards torque during the subsequent contraction of the dorsal muscles (E), which enables the person to rotate around their ankles (F). The sequence of activation of the muscles is indicated by the numbers 1 to 4.

may either rotate backwards around their ankles, moving their CoM in the same direction as the platform movement so as to realign their CoM with the new position of the feet (Horak and Nashner, 1986); or the person may take a step forwards, moving their CoM in the opposite direction to the platform translation (Burleigh et al., 1994; Maki et al., 2003).

3.2.1 Moving the CoM in the same direction as the platform

To return to their initial standing posture, the person must rotate their entire body backwards around the ankles, keeping their legs and trunk aligned. This movement must comply with the same mechanical requirements as voluntary movements: it requires backwards rotational momentum of the body around the ankles, and therefore calf muscle contraction, but also backwards rotational momentum of the trunk around the hips, and therefore contraction of the dorsal trunk muscles. Indeed, the calf muscles do not exert torque on the trunk around the hips. Therefore, if only the calf

muscles contract, then the rotational momentum of the trunk around the initial position of the hips is unchanged: due to its inertia, the trunk therefore rotates forwards in the external frame of reference as the legs rotate backwards. The person therefore flexes at the hips (Fig. 8 B). Maintaining the trunk aligned with the legs as the person rotates backwards therefore requires both an increase in the backwards rotational momentum of the body around the ankles, through calf muscle contraction, and an increase in the backwards rotational momentum of the trunk around the hips, through dorsal trunk muscle contraction. Such concurrent contraction of the dorsal muscles is indeed observed after a backwards platform translation (Horak and Nashner, 1986).

However, just after the platform translation, the person's CoM is further forwards than in the normal standing posture, which limits the net backwards torque around the ankles. This net torque could therefore be increased by increasing the initial backwards acceleration of the CoM. This can be performed by initially contracting the calf muscles (which accelerate the CoM backwards), without contracting the dorsal trunk muscles (which accelerate the CoM forwards). Indeed, it is observed that after a backwards platform translation, the calf muscles contract before (Fig. 11A) then throughout (Fig. 11B) the contraction of the dorsal trunk muscles (Horak and Nashner, 1986). This allows the person to recover their normal standing posture (Fig. 11C). If we take into consideration the knee, then the same analysis shows that the movement also requires contraction of the dorsal thigh muscles, and that leaning can be made more efficient by contracting first the calf muscles, then the dorsal thigh muscles, and finally the dorsal trunk muscles (Fig. 11B). This sequencing of activity is indeed observed (Horak and Nashner, 1986).

Both the systematic recruitment of the dorsal muscles after a backwards platform displacement, and their temporal sequencing emerge during development: they are not observed in prewalking infants, but are seen in children with a few years' walking experience (Burtner et al., 1998).

The initial backwards acceleration of the CoM could be further increased by additionally contracting the abdominals at the onset of movement, however this would cause the hips to flex. The contraction of the abdominals is therefore not observed after a slow backwards platform translation, presumably because the CoM acceleration induced by calf muscle contraction is sufficient. However, when the speed of the platform translation increases above a subject-specific threshold, then the abdominals are additionally recruited before the contraction of the calf muscles (Runge et al., 1999), as shown in (Fig. 11D). This accelerates the hips backwards and causes the trunk to rotate forwards (Fig. 11E). The person therefore moves their CoM to a position vertically aligned with the centre of their feet, but does not recover a straight posture until substantially later (Fig. 11F).

3.2.2 Moving the CoM in the opposite direction to the platform

According to the stabilization hypothesis, if the postural reaction cannot or does not counteract the perturbation by displacing the CoM in the same direction and by the same amount as the platform translation, then the person cannot keep their balance. Thus if the backwards acceleration of the CoM through the combined contraction of the abdominal and calf muscles is insufficient to recover the initial posture, then the person must fall.

However, a common response that is observed when balance is challenged is simply to take a step in the opposite direction to the platform movement, for example to take a step forwards in response to a backwards platform translation, and thereby to prevent a fall (Maki et al., 2003). When stepping forwards in response to a backwards platform translation, the initial forwards position of the CoM

relative to the feet due to the platform displacement should not be corrected for, but on the contrary may be exploited so as to provide forwards torque for taking the step. Thus, after a backwards platform translation, the calf muscle contraction should be smaller when the person responds by taking a step forwards than when the person responds by rotating backwards around the ankles. This reduced calf muscle contraction is indeed observed (Burleigh et al., 1994).

The response to a perturbation by an external force can thus involve displacing the CoM either in the same direction or in the opposite direction to the platform translation. Both responses may ensure balance, and both responses must comply with the same requirements as voluntary movements: they therefore both involve a change in the contraction of the lower leg muscles, which induces ground reaction torque, and their efficiency may be increased by a temporal organization of muscular contraction which initially accelerates the CoM in the appropriate direction for movement.

3.2.3 Heightened risk of falling in the elderly and in Parkinsonian patients

Thus, preventing a fall might actually rely on the capacity to move the CoM rather than to immobilise it. Indeed, elderly subjects (Speechley and Tinetti, 1991) and Parkinsonian patients (Allen et al., 2013) are known to be more at risk of falling than young subjects, yet their capacity to maintain their CoM immobile in quiet standing is comparable to that of young subjects (Schieppati et al., 1994). However, they cannot maintain their CoM as far forwards nor as far backwards from its normal position as young subjects. The range of CoM positions that can be maintained in quiet standing thus decreases with age and with the severity of Parkinson's disease. Moreover, the forwards acceleration of the CoM in gait initiation, as well as the subsequent walking speed, is reduced with age and with Parkinson’s disease (Halliday et al., 1998; Mancini et al., 2016). Thus, although the elderly and Parkinsonian subjects are quite as capable as young adults of maintaining their CoM immobile during quiet standing, we suggest that their higher risk of falling is due to a limited capacity to move when this becomes necessary to prevent a fall.

4 Discussion

4.1 Posture is adjusted in view of mobility rather than immobility

The ability to prevent falling is usually assumed to require immobilizing the CoM at a unique equilibrium position. However, in quiet standing the CoM may be stabilized over a range of positions. The posture that is typically adopted allows for immediate torque to be induced by muscular contraction. The net torque is indeed the sum of the torque of weight, which cannot be changed immediately by muscular contraction and is therefore initially determined by the position of the CoM in quiet standing, and the ground reaction force, which immediately follows changes in the contraction of the lower leg muscles, but which is limited by the extent of the feet. We therefore argue that the position of the CoM is controlled in view of movement rather than immobility. Thus, when performing a well-practiced movement, the temporal organization of muscular contraction patterns does not serve to immobilize the CoM despite movement. On the contrary, it initially accelerates the CoM in the appropriate direction, such that one’s own weight may be used to provide torque for movement. This capacity to move the CoM, rather than to immobilize it, actually seems to be crucial to prevent falling when the standing posture is perturbed by an external force.

4.2 Implications of postural adaptation for motor control theories

Motor control theories are typically organized around the notion of motor redundancy: from the observation that the human body comprises numerous joints and muscles, it is assumed that the human motor system has more degrees of freedom than are needed to perform any given task. The neural organization of movement is therefore thought to consist in adding constraints to movement patterns, so as to solve the degrees of freedom problem. Two different hypotheses are put forwards as to the type of constraints that the nervous system imposes upon movement patterns. The first hypothesis is that the nervous system composes movement from fixed building blocks, called synergies (Bizzi et al., 2008). The second hypothesis is that the nervous system choses the movement which minimizes various cost functions; this alternative is called optimal control (Todorov and Jordan, 2002).

Our analysis suggests however that the degrees of freedom required to perform varied movements are actually larger than generally appreciated. For example, both leaning the trunk backwards (Fig. 9A-E), and rotating the entire body backwards around the ankles (Fig. 11A-C) require activation of the calf and dorsal trunk muscles. The concurrent activation of the calf and dorsal trunk muscles has therefore been suggested to be a synergy common to both voluntary movement and the response to platform perturbation (Massion et al., 2004). However, we have shown that, for a given trunk muscle contraction, the contraction of the calf muscles must be larger for rotating the entire body backwards than for leaning the trunk backwards. Since these two movements have different mechanical requirements, they cannot be performed with a fixed ratio of muscular contraction: two degrees of freedom are therefore required in order to perform these two movements. The same holds when additional joints are taken into consideration: in order to produce movements with diverse mechanical requirements, diverse ratios of muscular contraction are required.

Moreover, we have only presented the patterns of muscular contractions that can fulfil these requirements when the person is standing on solid ground. As soon as the conditions of the support change, so do the patterns of muscular contraction required to induce the appropriate change in the reaction force of the support. Indeed the muscular contraction patterns that are observed when someone performs a given movement are different when the person is sitting (Horak et al., 1992), crouching (Macpherson et al., 1989), kneeling or holding onto a stable support (Cordo and Nashner, 1982; Marsden et al., 1981). Producing the appropriate mechanical effect therefore requires a whole new set of muscular contraction patterns for each condition of support. Our analysis of the mechanical requirements for movement therefore suggests that the number of degrees of freedom necessary for skillful muscular control might be larger than generally appreciated. In organizing movement which complies with the mechanical requirements for moving, additional constraints such as synergies or cost functions might therefore not be necessary.

Finally, the temporal sequencing of activation which allows one’s own weight to be used as a propulsive force emerges over the course of development both for walking and for balancing responses (Burtner et al., 1998; Ledebt et al., 1998), but for every new movement that is practiced, it seems to be learned anew. Thus, with skill learning, acrobats seem to adapt their posture in handstands (Clément and Rézette, 1985), and gymnasts seem to adapt their postural adjustments (Pedotti et al., 1989), such that skillful movements may exploit the torque of gravity. Further evidence for this comes from the literature on skill learning, in which the movements of beginners are seen to use in phase coordination of the various body segments, whereas the movements of experts

have a temporal sequencing which allows them to better exploit the work of gravity (Delignières et al., 1998). Thus, the way in which a movement is performed changes with skill learning, such that the movement patterns of beginners and experts cannot result from a fixed set of constraints: they cannot be obtained as a combination of fixed synergies, nor can they both be the minimum of a fixed cost function.

In conclusion, the consideration of the mechanical requirements for movement has led us to describe movement in terms of changes in momentum. In this perspective, postural control is seen as the ability to provide impetus to movement, which requires fine and flexible control of the different muscles. The importance of such versatility has been put forwards by Bernstein, who, by analogy with the human body, noted that "In many cases a more flexible instrument, which is certainly much more challenging to work with, has unquestionable advantages in its flexibility and fine results" (Bernstein, 1996).

5 Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

6 Author Contributions

Both authors have jointly contributed to the development of the ideas presented and to the writing of the manuscript.

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