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COMMENTARY

Yank: the time derivative of force is an important biomechanical variable in sensorimotor systems

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ABSTRACT

The derivative of force with respect to time does not have a standard term in physics. As a consequence, the quantity has been given a variety of names, the most closely related being 'rate of force development'. The lack of a proper name has made it difficult to understand how different structures and processes within the sensorimotor system respond to and shape the dynamics of force generation, which is critical for survival in many species. We advocate that $\partial\vec{F}/\partial t$ be termed 'yank', a term that has previously been informally used and never formally defined. Our aim in this Commentary is to establish the significance of yank in how biological motor systems are organized, evolve and adapt. Further, by defining the quantity in mathematical terms, several measurement variables that are commonly reported can be clarified and unified. In this Commentary, we first detail the many types of motor function that are affected by the magnitude of yank generation, especially those related to time-constrained activities. These activities include escape, prey capture and postural responses to perturbations. Next, we describe the multi-scale structures and processes of the musculoskeletal system that influence yank and can be modified to increase yank generation. Lastly, we highlight recent studies showing that yank is represented in the sensory feedback system, and discuss how this information is used to enhance postural stability and facilitate recovery from postural perturbations. Overall, we promote an increased consideration of yank in studying biological motor and sensory systems.

KEY WORDS: Biomechanics, Muscle, Spindle

Introduction

In this Commentary, we assert that the derivative of force with respect to time, $\partial\vec{F}/\partial t$, is an important quantity at all scales within sensorimotor systems. We advocate that this quantity be termed 'yank' (see Glossary) to underscore its significance within biological motor systems. Yank can be used in the measurement of the time variation of propulsive force during movements ranging from locomotion to escape, of forces generated by muscles within the musculoskeletal system, and of the responses of sensory organs that are used in motor reflexes.

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The time derivative of force has no standard term in physics. This is in contrast to the time derivatives of displacement – velocity, acceleration and jerk – which have been used extensively in biomechanical analyses of biological motor systems (Winter, 2009). Providing names for these quantities clarifies biomechanical analyses, as their definitions are based on rigorous mathematical formulations. Further, defining the mathematical constructs of these variables unifies analyses because the variable meaning is identical no matter the conditions or scale at which they are measured or modeled. This is important because measurement methodologies may influence the numerical estimates of yank, and a formal definition would clarify the actual quantity that is estimated. For the same reasons that it is useful to define multiple time derivatives of kinematic variables, we propose that $\partial\vec{F}/\partial t$ be termed yank, and defined as a continuous time variable or time series that represents the first time derivative of force, or the rate of change in force over time. Note that we denote the force as a vector to generalize to conditions where force is not just a scalar value.

Yank has not been well defined in biological motor systems, in part because the properties of major components of the motor system – namely, muscle and sensory organs within muscle – have been studied based on the relationship between steady-state kinematics and steady-state force, typically after a perturbation has been imposed. For example, virtually all characterizations of muscles and muscle spindle sensory organs (see Glossary) describe their length (i.e. elastic) and velocity (i.e. viscous) response during the steady-state period after the initial transient responses have disappeared, whether the response is force for muscle or neural firing rate for sensory afferents (Houk and Rymer, 1981; Houk et al., 1992; Lin and Rymer, 1993; Matthews, 1963). However, the transient properties of force generation and sensory response are immensely important, possibly more so than the steady-state properties. In particular, many motor tasks like ballistic motions or responses to impulse-like perturbations require that mechanical actions occur within an initial small interval of time to complete the task, or the task cannot be successfully performed. Quantities that are mathematically linked to the time derivatives (i.e. rate of change) enable better measurement and assessment of those transient properties, and are currently reported in the literature using a variety of terms, often including the word 'instantaneous' (i.e. 'instantaneous rate of force development') (Li et al., 2015).

This Commentary is organized by spatial scale. Our aim is to show connections between micro- and macro-structures and processes in sensorimotor systems, using a consistent definition of yank at every scale. We first detail the importance of yank for organismal motor behavior, specifically in ballistic movements, such as jumping and sprinting, and in reflexive actions, such as tripping or postural perturbations. We then focus on musculotendon dynamics and muscle contractile processes, and describe how the properties and the plasticity of specific anatomical structures influence the ability to produce yank. Lastly, we discuss how

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Glossary

Catch-like force enhancement
The rapid increase in force generated by a muscle when two action potentials activating the muscle are closely spaced in time (i.e. a doublet).

Golgi tendon organs
Sensory organs located within the tendon of a skeletal muscle.

Ground reaction force
The force that is produced by the environment (usually the ground) when a body part is in contact with the environment.

Isometric
In the context of muscle physiology, this is equivalent to the static condition, during which there is no change in length of a muscle or no change in angle of a joint.

Joint torque or moment
In biomechanics, muscle force multiplied by the muscle's moment arm (i.e. lever arm) is equal to the joint moment.

Muscle spindle sensory organs
Sensory organs located within the skeletal muscle.

Rate of force development
The phrase that describes a quantity equal to the increase in muscle force, ground reaction force or joint moment divided by the time interval of that increase.

Yank
The first time derivative of force.

yank is represented in the sensory system and influences spinal reflexes. In total, these observations indicate that yank is an important quantity for control of posture and movement.

Yank magnitude is an important factor for completing and optimizing rapid movements

The relationship between the performance of rapid movements and ability to survive has been studied across a wide range of species. For ambush predators, the ability to be at a target position in the least amount of time maximizes the probability of prey capture (deVries et al., 2012). Conversely, a prey animal maximizes its chances of survival by having an escape response that is large enough and fast enough to enable it to leave the target area before the predator strikes. The idea that metrics of motor performance predict intra-species survival has been studied directly in snakes and lizards. For example, in adult garter snakes, 'maximal burst speed' significantly predicts survival, whereas endurance and maximal steady-state speed do not (Bennett and Huey, 1990). Additionally, in juvenile lizards, significant selection was found for 'burst velocity' and 'initial velocity' (Miles, 2004). More generally, motor behaviors involving predation or escape have been called 'time-limited movements', and yank has been found to be a key determinant of motor performance in these behaviors (Rosario et al., 2016).

More specifically, in movements that involve leaving the ground, such as jumping or leaping, takeoff velocity needs to be maximized to achieve the greatest distance (Garcia-Ramos et al., 2015). We have been studying vertical jumping mechanics in kangaroo rats, which are capable of vertically jumping to 10 times their standing hip height (Biewener and Blickhan, 1988; Schwaner et al., 2018) (Fig. 1). To accomplish this high performance, the kangaroo rat generates large ground reaction forces (GRFs; see Glossary) in a short time period, which translates to a large yank magnitude. At the organismal level, yank can be calculated from the time recording of GRF, which can then be related to the metrics of performance, such as time to takeoff and takeoff velocity.

In jumping, maximizing takeoff velocity while minimizing ground contact time could involve a tradeoff because time is necessary to accelerate the body mass. In other words, the magnitude of the mechanical impulse (i.e. the area under the force versus time plot) that produces the velocity at takeoff involves both the magnitude and duration of the force. With an increase in yank, force magnitude will increase but its duration decreases, which offsets the effects of increased impulse magnitude. To address the influence of yank on this tradeoff, a simple model of vertical jumping can be used (Fig. 2). The body mass is acted upon by a vertical GRF (gravity is neglected to simplify the model) that has a time profile similar to the GRF time plot in Fig. 1 and is approximated as:

$$\mathrm{GRF}(t) = A(e^{t/\tau} - 1), \quad (1)$$

where t is time, A is a constant and τ is a time constant. Taking the time derivative of this equation, the left side yields yank as a function of time:

$$Y(t) = (A/\tau) \times e^{t/\tau}, \quad (2)$$

such that changes in τ change yank magnitude. If it is assumed that for a vertical jump, takeoff occurs at full extension of the joints (i.e. at a fixed displacement of the body mass) (Alexander, 1989), a larger yank (i.e. smaller τ) would shorten the amount of time to takeoff. For this model, the time at takeoff can be found by: integrating the body acceleration (GRF divided by mass) twice to obtain the body mass displacement as a function of time; and determining the time at which the displacement is equal to the takeoff displacement (takeoff time is marked with a cross in Fig. 2B).

Using the model in Fig. 2, we examined whether there was a benefit for takeoff time (i.e. a decrease) and takeoff velocity (i.e. an

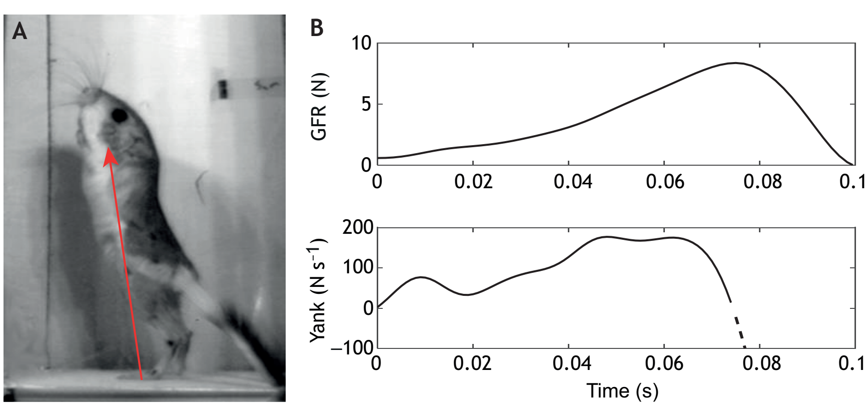

Fig. 1. Yank can be derived from time recordings of ground reaction force (GRF) during motor behaviors. (A) In our previous study, kangaroo rats jumped over a vertical barrier from a standing posture (Schwaner et al., 2018). The GRF vector (red arrow) was measured using a force plate. The mass of the animal shown is 0.12 kg, corresponding to a GRF of 1.2 N at the initiation of the jump. (B) Yank is calculated from the measured GRFs (only the vertical component is shown). Only the first portion of negative yank values before the feet left the ground is shown (dashed line) so that the positive yank generated can be appropriately scaled on the plot.

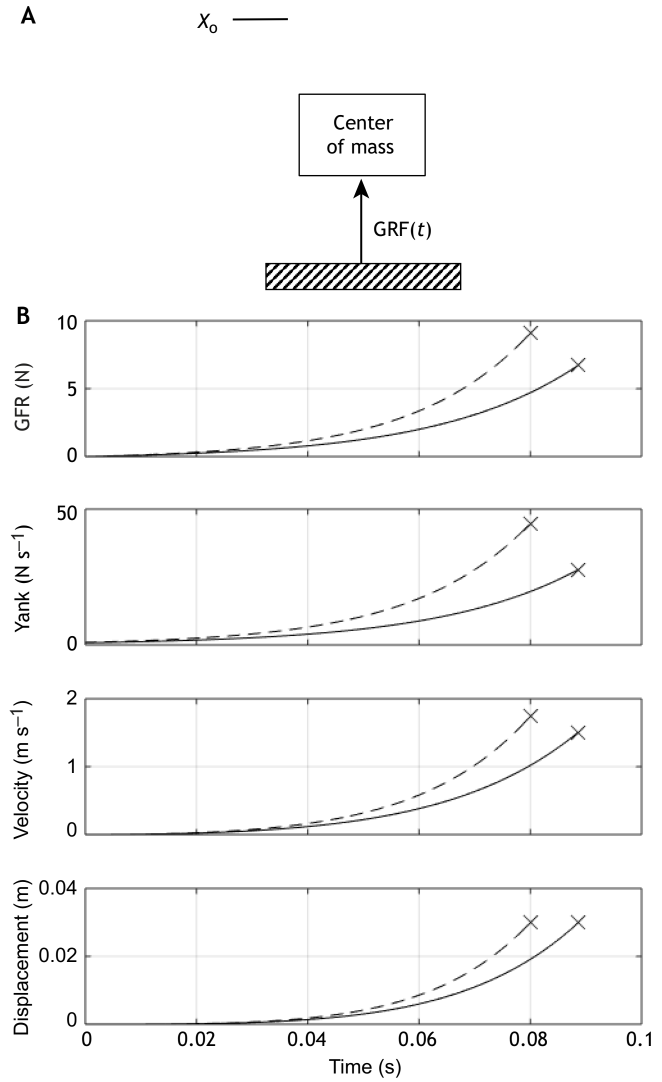

Fig. 2. A simple model showing how changes in yank magnitude change behavioral outcomes during a jump. See main text for details. (A) The center of mass of an animal is accelerated upwards by the vertical GRF until the takeoff point, X_o. Gravity and non-vertical forces are neglected for simplicity. (B) The GRF is assumed to be exponential (see Eqn 1) and the resulting yank, position and velocity are shown. The two cases shown are with nominal values (solid line) and with a 20% decrease in the exponential time constant (dashed line). The time of takeoff is indicated by a cross. Note the time to takeoff decreases and jump velocity increases with an increase in yank. Model parameters (Eqn 1) are: A=0.2 N, τ=0.025 s and body mass=0.1 kg.

increase) due to increased yank. Yank was increased by decreasing the time constant in Eqn 2, which can be related to the time constants associated with activation and excitation dynamics (Zajac, 1989). We found that with a 20% decrease in the time constant, the takeoff time decreased by 10% and the takeoff velocity increased by 16% (Fig. 2B). Thus, increased yank is a potential mechanism to avoid the tradeoff between decreasing contact time and increasing takeoff velocity.

The role of yank is also critical in human motor performance. The term ‘rate of force development’ (RFD; see Glossary), which is closely related to yank (see ‘The organismal level’, below), is extensively used in the human strength and conditioning literature and has provided valuable insight into how changes in the musculoskeletal system affect motor performance (Maffiuletti et al., 2016; Rodríguez-Rosell et al., 2018). It has been shown that athletic performance and recovery during rehabilitation are closely related to the improvement in RFD, more so than to maximal strength measures (Buckthorpe and Roi, 2017). Other examples in the area of sports science include: the dependence of maximal cycling performance upon muscle deactivation rate, which is reflected in the maximal negative yank (Neptune and Kautz, 2001); and the ability of elite sprinters to generate large yank (i.e. larger GRF with shorter contact time), relative to athletes using running-specific prostheses, which results in higher running speed (McGowan et al., 2012). Yank is also important in reflexive motor behaviors. For example, the ability to recover from tripping is highly dependent on generating a large peak yank in the stance leg to change the angular momentum of the body mass (Pijnappels et al., 2005). Moreover, during discrete perturbations to standing balance in humans, a large yank is produced by the combination of the initial muscle stretch and intrinsic short-range stiffness of muscle. This response provides a rapid and transient stabilization of the body to compensate for time delays in neural reflex pathways (De Groote et al., 2017). Furthermore, in cats, impaired balance ability after sensory neuropathy emerges from the inability to generate a rapid rise in balance-correcting muscle activity and joint torque (see Glossary); that is, the ability to produce high yank in muscle is impaired (Lockhart and Ting, 2007).

It should be noted that the relationship between yank and the kinematic variables of length, velocity, acceleration and jerk depends upon the mechanical properties of the body and environment (Ting and Chiel, 2017). In many of the situations explained above, such as jumping or running on a hard surface, inertial loads dominate, and the net force is equal to the force propelling the body center of mass, which can be measured by devices such as a force plate. In this case (as in Fig. 2), the propulsive force is equal to mass multiplied by acceleration, and yank of the propulsive force is proportional to jerk (the third time derivative of displacement) (Alexander, 1989). However, in aqueous environments, the forces that are needed to generate motion can be dominated by viscous forces (i.e. drag). These forces resisting motion are proportional to velocity; thus, yank of the propulsive force (which generates the motion) is proportional to acceleration of the mass (Vogel, 1996). In addition, the ability to generate large yank is of foremost functional importance when movements are made on substrates other than a hard surface. For example, the ability of some lizards to walk on water is enabled by generating a large enough yank during the initial foot contact with water (the ‘slap phase’) to create an air pocket surrounding the foot (Hsieh and Lauder, 2004; Glasheen and McMahon, 1996).

Yank is an important quantity at all scales of the motor system

Skeletal muscles are responsible for generating the active forces, and thus yank, within the musculoskeletal system. The contractile processes that lead to muscle force generation are multiscale in nature: the time-varying macroscopic joint moments are due to underlying kinetics of actin–myosin protein interactions and conformational changes. Thus, yank is influenced by each of the multiple processes that are involved in muscle contraction (Fig. 3).

The organismal level

As discussed previously, yank can be measured at the organismal level using force plates, which measure the GRF. Additional *in vivo* measurements are often performed at the joint moment level [$M(t)$ in Fig. 3], especially in humans. These measurements are usually

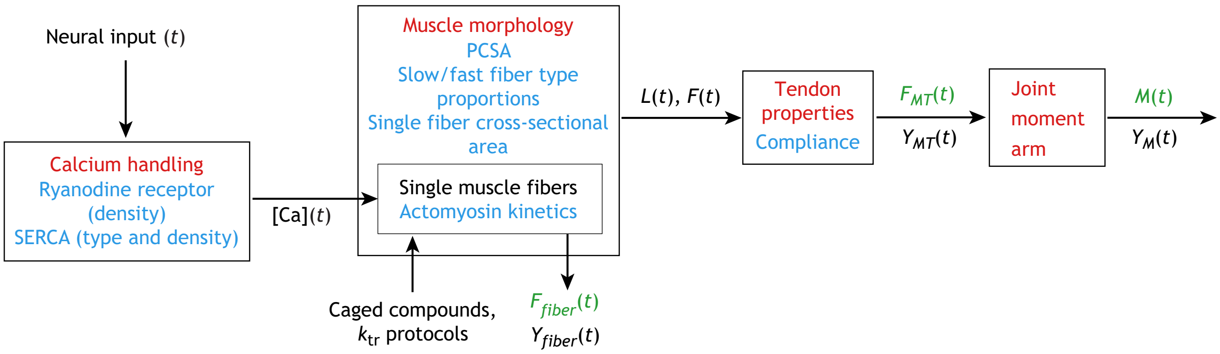

Fig. 3. The multi-scale anatomical structures and processes that determine the magnitude of yank. The structures/processes are indicated in red. The plasticity within each structure which influences yank is represented by changes in specific variables, indicated in blue. Yank can be calculated using the measured variables from *in vivo*, *in situ* or *in vitro* experiments, indicated in green. *t*, time; [Ca^{2+}], intracellular calcium concentration; $F_{fiber}(t)$, single fiber force (measured *in vitro*); $Y_{fiber}(t)$, yank of fiber force; $L(t)$ and $F(t)$, muscle length and force; $F_{MT}(t)$, musculotendon force; $Y_{MT}(t)$, yank of musculotendon force; $M(t)$, joint moment (measured *in vivo*); $Y_M(t)$, yank of joint moment; PCSA, physiological cross-sectional area; SERCA, sarco/endoplasmic reticulum; and k_{tr}, time constant of force recovery.

made with dynamometers during isometric conditions (see Glossary), and the assessment involves estimation of the RFD (Aagaard et al., 2002), usually by a two-point estimation over a specified time interval:

$$\mathrm{RFD} = (F_{t_1} - F_{t_{\mathrm{onset}}})/(t_1 - t_{\mathrm{onset}}), \tag{3}$$

where F is force, t_{onset} is the time of the start of force rise and t_1 is a specific point in time (e.g. 50, 100 or 200 ms after onset) (Maffiuletti et al., 2016). Using this definition, RFD is the average yank within the specified time period (see fig. 8 of Maffiuletti et al., 2016).

We advocate that researchers explore the use of yank to complement RFD assessments, such as defining the time of transition between the initial and rapid rise phases (by examination of the time derivative of yank) or using time of peak yank. It is important to note that because calculation of yank involves taking the time derivative of force measurements, the estimate of yank is susceptible to the amplification of noise in the force recording, from either electrical sources (i.e. 60 Hz noise) or mechanical causes (e.g. the resonant frequency of a force plate). However, well-accepted numerical techniques can be used to optimize the derivative calculation by minimizing and quantifying the effects of noise and/or preserving actual transients in the recording. These include applying an appropriate bandpass or notch filter for known frequencies of noise and/or using splines for the derivative estimate (Woltring, 1985).

The musculotendon level

At the whole musculotendon level, in either *in situ* or *in vitro* preparations, a commonly made measurement that directly relates to yank is the twitch response. In a twitch, the rates of force development and relaxation correspond directly to positive and negative yank, respectively, and are indicative of alterations in the contractile machinery due to pathologies, training or aging (Aagaard et al., 2002; Bellumori et al., 2013; Penailillo et al., 2015). Often, specific instances in time are used as metrics to characterize the twitch dynamics. For example, 'half-rise time' and 'half-relaxation time' are the instances in time when force reaches half-maximal force during the rising and falling phases, respectively (Rehwaldt et al., 2017). In addition, baseline force, from which the maximal force is referenced, can change during the course of the experiment, and a long relaxation phase (i.e. small slope) can make the estimate of half-relaxation time difficult. Reporting yank would resolve these two issues: a derivative is less sensitive to changes in baseline levels, and the peak negative yank value would be clear. With this perspective, studies reporting 'maximal rate of force development' (Girard and Millet, 2009) could simply report maximal yank. We advocate the use of a standard methodology for numerical differentiation on the muscle and musculotendon force recordings, removing ambiguity in the reported results.

The cellular level

At the cellular level, with experiments performed on single muscle fibers, yank is used widely to reveal the kinetics of actomyosin (i.e. crossbridge) interactions. Namely, the dynamics of the force response to a sudden perturbation are related to the kinetic rate constants of crossbridge cycling (Fig. 3). If the perturbation is a rapid shortening and re-lengthening in fiber length, k_{tr} is the time constant of the force redevelopment, which is assumed to have first-order dynamics of the form (Wang and Kawai, 2013):

$$F_{\mathrm{recovery}}(t) = F_{\mathrm{ss}}\left(1 - e^{-t/k_{\mathrm{tr}}}\right), \tag{4}$$

where F_{recovery} is force following the perturbation, t is time and F_{ss} is the steady-state force following the perturbation. As with Eqn 2, the derivative of Eqn 4 is equal to yank, which increases as k_{tr} decreases. Physiologically, the significance of k_{tr} is that it is assumed to be proportional to the ratio between crossbridge attachment and detachment rates (Campbell, 2006). Similarly, if the perturbation is the rapid release of a 'caged' compound (commonly ATP, phosphate or calcium), the transients of the force response are related to the kinetics of the specific step within the crossbridge cycle, because changes in compound concentration shift the equilibrium of that step (Homsher et al., 1997). In general, in studies involving length step and caged compound perturbations, it is the time dependence of the force response that is important, and yank is a direct metric of the time dependence of force.

Mechanisms influencing yank

A comprehensive review of the mechanisms influencing RFD, which are the same mechanisms influencing positively valued yank, has been published recently (Maffiuletti et al., 2016), so they will only be briefly described in the following paragraphs, with additional discussion about the deactivation process (influencing negative yank) and the effects of muscle–tendon interactions. These mechanisms are from all spatial scales, from the molecular processes of calcium release and uptake and of crossbridge cycling to the integrative processes of muscle–tendon interactions, providing the motor system with multiple means to influence yank.

Two of the main determinants of yank are muscle activation and deactivation through the processes of calcium release and uptake, controlled via neural input (Fig. 3) (Wahr and Rall, 1997). The initial burst of neural activity can be increased via training, and it is likely that this is due to a higher frequency of doublets (the closely spaced occurrence of action potentials). Doublets engage the 'catch-like' force enhancement property of muscle (see Glossary), which increases yank by allowing muscle force to reach a higher level more quickly (Van Cutsem et al., 1998; Binder-Macleod and Kesar, 2005). In the release of calcium, the density of ryanodine receptors on the surface of the sarcoplasmic reticulum can change with training, such that there is an increased calcium release rate (Saborido et al., 1995). For deactivation, sarco/endoplasmic reticulum Ca^{2+}-ATPase (SERCA) is a main determinant of calcium uptake rate and, consequently, the time constant of muscle relaxation (Periasamy and Kalyanasundaram, 2007). The kinetics of calcium uptake is influenced both by the isoforms expressed, with SERCA1 having slower kinetics than SERCA2A, and by the density of SERCA. Changes in the density and proportion of the two isoforms can be induced by training (Kinnunen and Mänttäri, 2012).

In the muscle contractile processes, crossbridge cycling rates have been estimated to be as much as 4 times slower in type I versus type II muscle fibers (He et al., 2000). As a consequence, it has long been assumed that a higher proportion of type II fibers, which can be induced via training, contributes to a larger yank (Methenitis et al., 2017). Moreover, a key to understanding how the plasticity of fiber type influences yank is that when muscles are activated from rest, the slack of the tendon and lower compliance of the tendon's toe region can cause rapid shortening of the muscle (Edman and Josephson, 2007; Krylow and Rymer, 1997). Through the force–velocity relationship, the muscle force is substantially reduced due to muscle shortening, and much more so in type I fibers versus type II fibers. Thus, fiber type has an important role in determining positive yank, especially for muscle with long compliant tendons which are highly extensible (Edman and Josephson, 2007). Tendons can also affect negative yank. A recent modeling study showed that the most prominent outcome of adding series-elasticity to a half-sarcomere model is to greatly increase negative yank (Campbell, 2016).

In absolute terms, muscle size, as measured by physiological cross-sectional area (PCSA), is a primary determinant of yank magnitude. PCSA is a scalar term for force in all muscle models (Zajac, 1989). For example, in the simple model presented in Fig. 1 and Eqns 2 and 3, the A term is a scalar which is directly related to PCSAs of the muscles involved.

Yank is represented and plays an important role within the sensorimotor feedback system

The closed-loop response of perturbations to posture is a multi-scale response that depends upon the intrinsic properties of muscles, sensory afferents and the reflexive pathways to muscles (Fig. 4). Yank is an important quantity for understanding many sensory signals during movements and in response to postural perturbations. A variety of somatosensory afferent firing rates in response to stimuli have been characterized based on the rates of change of force (yank), mechanical stress or moment. For example, cutaneous sensors in rat skin respond to the rate of change in skin stress during skin stretch (Grigg and Del Prete, 2002). In particular, rapidly adapting afferents exhibit a strong response at the onset of stretch that depends on the rate of change of stress (Grigg et al., 2004;

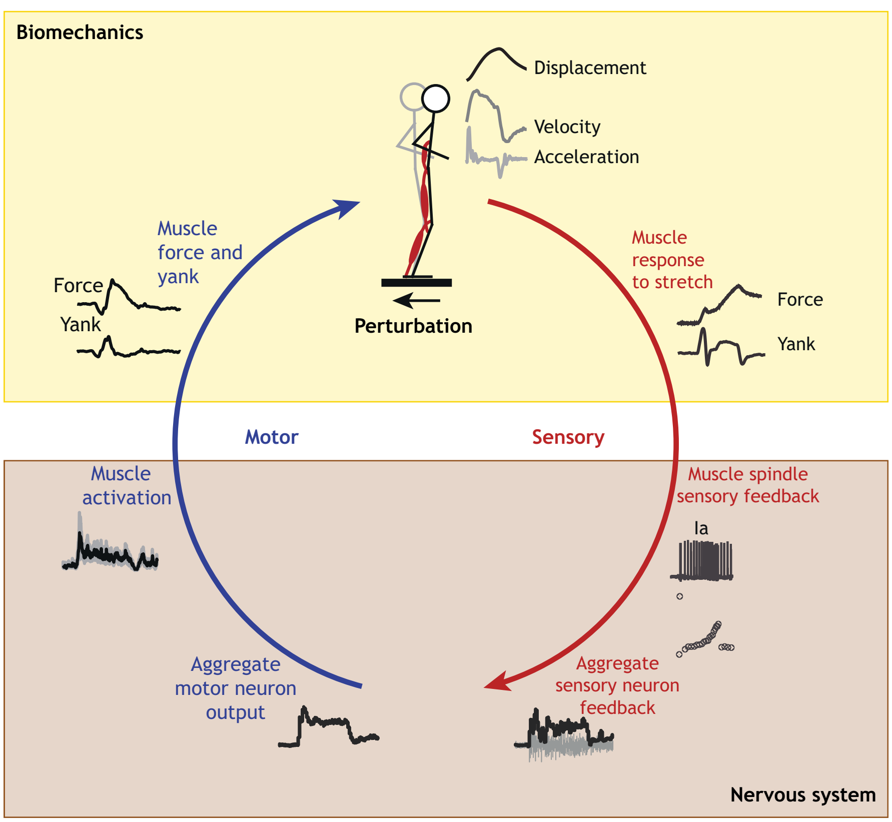

Fig. 4. Proposed role of yank in the sensorimotor feedback loop. The initial rise in yank caused by the postural perturbation is carried through the feedback loop and leads to faster reactive muscle force responses to counteract the perturbation. When a postural perturbation occurs, muscle fibers are stretched and have initial force and yank responses that drive muscle spindle Ia afferent sensory feedback. This sensory feedback, along with that from other receptors, drives motoneuron potential changes with initial bursts of activity. These motoneuronal potential changes lead to an initial burst in electrical activation of muscles resembling the yank in the stretched muscle, which in turn causes rapid muscle contraction, facilitated by the catch-like property of the muscle, resulting in a high initial yank of the balance-correcting muscle force.

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Robichaud et al., 2003). In addition, rat whiskers provide information from interactions with the environment, with the rate of change in the moment at the base of the whisker providing crucial information for object recognition (Birdwell et al., 2007). Another example is provided from work on cats – the firing of Golgi tendon organs (GTO; see Glossary) at the muscle–tendon junction depends not only on muscle force but also on yank, especially during non-steady activation when force and yank are time varying (Jami et al., 1985). The 'dynamic sensitivity', or the sensitivity to the time derivatives of force, i.e. yank, is a predominant factor influencing the discharge rate of the GTO, in contrast to the mean force sensitivity.

Muscle spindle sensory organs provide essential information for movement control and have properties that appear to reflect the yank and force within muscle fibers. Intrafusal muscle fibers (i.e. fibers within muscle spindle sensory organs) have the same force generation and stretch response properties as extrafusal muscle fibers. Classically, as determined through analysis of steady-state firing rates throughout an imposed stretch, the muscle spindle has been explained as encoding muscle length and velocity (Houk et al., 1992; Matthews, 1963). We recently showed that during stretch of relaxed muscles, muscle spindle Ia afferent responses can be explained and predicted by linear combinations of muscle fiber force and yank (Fig. 5) (Blum et al., 2017, 2019). In particular, the initial burst of muscle spindle firing was accounted for by the initial transient rise in muscle force due to short-range stiffness. Because muscle short-range stiffness increases yank and decreases muscle length change, the dependence of muscle spindle firing rate on yank and force can be clearly dissociated compared with that observed during steady-state conditions. Further, the history dependence of the muscle short-range stiffness exactly matches the history dependence of muscle spindle firing rate. This history dependence causes a non-unique (i.e. not one-to-one) relationship between muscle length and muscle spindle firing rate.

While yank seems to be represented in both muscle spindles and GTOs and this could yield redundant sensory information, it is worth noting that yank within a muscle can be generated either by voluntary muscle activation or by the involuntary response to a perturbation. Usually, the voluntary yank generation will result in muscle shortening (due to tendon slack and compliance) and activity in the GTO, whereas involuntary yank generation occurs as a result of a perturbation from the environment that lengthens the muscle. Thus, we hypothesize that the two different sensors could distinguish the source of yank, voluntary activation for GTOs and perturbations for muscle spindles; this could allow the organism to shape the reflex response appropriately. Consistent with this idea is that force feedback from the GTOs helps to compensate for muscle fatigue (Kirsch and Rymer, 1992) and is responsible for about 30% of the activation in cat hindlimb muscles during level walking (Donelan et al., 2009).

The yank-based signals from muscle spindle sensory organs are likely to be crucial in stabilizing body posture in the face of relatively long neural transmission times. It is well established both experimentally and theoretically that neural transmission time within the sensorimotor loop adds phase delays and impacts stability (Rack, 1981), both of which can cause the mass of the limbs to have more oscillatory motion (Stiles, 1983). Our work implicates yank signals in driving the initial bursts that appear in long-latency balance-correcting muscle responses prior to substantial changes in muscle length (Blum et al., 2017, 2019; Lin and Rymer, 2001; Lockhart and Ting, 2007).

We propose that the initial burst in muscle spindle firing caused by yank in response to muscle stretch drives an initial burst in muscle activity (De Groote et al., 2017), which in turn increases the yank generation for balance corrections, facilitated by the catch-like property of muscle (Binder-Macleod and Kesar, 2005) (Fig. 5). As such, yank signals can compensate for the undesirable effects of neural delays by providing signals that predict the magnitude of the perturbation (Insperger et al., 2013; Ting et al., 2009). This idea has a strong theoretical basis from classical control theory, in which higher-order derivatives are used as feedback signals to anticipate changes and increase damping of oscillatory motion that could result from the perturbation (Franklin et al., 2019). Indeed, the initial burst in muscle activity following a perturbation is lost after neuropathy that eliminates group I sensory afferents (GTO, cutaneous and muscle spindle Ia afferents), which reduces the rate

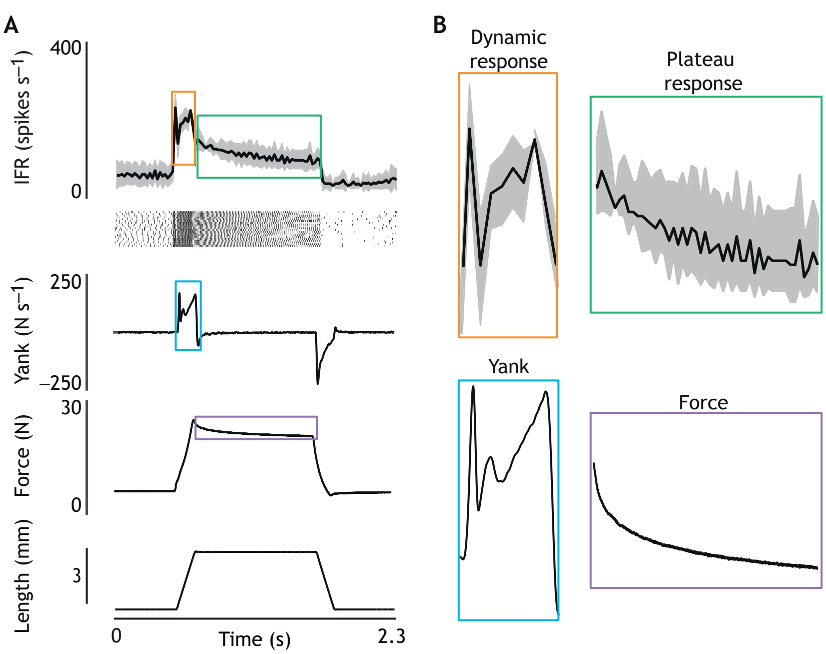

Fig. 5. Yank is encoded in the dynamic response of muscle spindle primary afferents. (A) A ramp–hold–release stretch protocol (bottom panel) is applied to the isolated, relaxed triceps surae muscle–tendon unit (MTU) of a cat, which causes a force and yank response in the MTU (middle panels), and a spiking response of the primary afferent neuron (top panel; IFR, instantaneous firing rate). (B) Enlargement of the boxed regions in A. The afferent firing rate closely resembles yank during the positive velocity ramp phase of the stretch and more closely resembles the force during the plateau phase of stretch.

of torque rise in a balance-impaired animal (Lockhart and Ting, 2007).

Conclusion

We advocate the use of the term yank, which is mathematically defined as the first time derivative of force. Throughout this Commentary, we hope to have provided evidence of the significance of yank to locomotor systems. Multi-scale analysis of yank can provide insight into the organization, evolution and plasticity of biological motor systems that allows them to cope with the constraints imposed by the environment, by the physics of skeletal motion and by the biological implementation of actuators and sensors. We believe that the mathematical basis of yank will advance the field of motor control because, methodologically, it will allow researchers to generalize metrics of motor performance to a greater extent relative to the most closely related terminology, RFD. Finally, understanding how yank is represented in the sensory system will allow us to elucidate the actions of sensorimotor feedback for posture and movement.

Competing interests

The authors declare no competing or financial interests.

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