Stretch-induced enhancement of mechanical power output in human multijoint exercise with countermovement

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M. Takarada, Yudai, Yuichi Hirano, Yusuke Ishige, and Naokata Ishii. Stretch-induced enhancement of mechanical power output in human multijoint exercise with countermovement. J. Appl. Physiol. 83(5): 1749–1755, 1997.—The relation between the eccentric force developed during a countermovement and the mechanical power output was studied in squating exercises under nominally isotonic load (50% of 1-repetition maximum). The subjects (n = 5) performed squatting exercises with a countermovement at varied deceleration rates before lifting the load. The ground reaction force and video images were recorded to obtain the power output of the body. Net muscle moments acting at hip, knee, and ankle joints were calculated from video recordings by using inverse dynamics. When an intense deceleration was taken at the end of downward movement, large eccentric force was developed and the mechanical power subsequently produced during the lifting movement was consistently larger than that produced without the countermovement. Both maximal and mean power outputs during concentric actions increased initially with the eccentric force, whereas they began to decline when the eccentric force exceeded ~1.4 times the sum of load and body weight. Video-image analysis showed that this characteristic relation was predominantly determined by the torque around the knee joint. Electromyographic analyses showed no consistent increase in time-averaged integrated electromyography from vastus lateralis with the power output, suggesting that the enhancement of power output is primarily caused by the prestretch-induced improvement of an intrinsic force-generating capability of the agonist muscle.

cross-bridge mechanism; prestretch; eccentric contraction; squatting exercise; knee extensor muscles

When contracting muscle is first stretched (prestretch) and then immediately allowed to shorten, it generally exhibits higher contractile performance than if it does without prestretch, e.g., enhanced productions of mechanical work and power in isokinetic and isotonic conditions, respectively. Such a phenomenon is seen in normal movements of various organisms, including humans, most frequently in the form of a countermovement. The countermovement consists of an initial shortening of muscle (eccentric action) and a subsequent, rapid reversal of the movement to produce shortening of muscle (concentric action). This rapid deceleration of the eccentric action gives rise to the generation of large force and thereby makes the following concentric action stronger.

The mechanisms underlying such a stretch-induced enhancement of mechanical performance have so far been a matter of controversy. Studies with single muscle fibers have suggested that an improvement of the force-generating capability occurs in interacting cross bridges (5, 10, 22), whereas studies on in situ contractions have insisted on the reutilization of elastic energy stored in the series elastic component (SEC) located mainly in tendon (3, 16).

In the companion paper (22a), we have shown that, in both human elbow flexors and frog single fibers, mechanical work production during an isokinetic shortening after a ramp stretch depends on the peak force developed during the stretch in a “biphasic” manner: it increases with the force until the force reaches a certain level, and then it decreases with the further increase in force, indicating the presence of an optimal eccentric force for the enhancement of work production. This suggests that some modification occurs in the contractile apparatus after stretch and plays a part in the enhancement of work production, because the elastic energy to be stored in the SEC would be directly proportional to the force on the SEC. Also, this suggests that similar mechanisms operate in contractions of single fibers and human single-joint movements in situ.

It has been unknown whether such a biphasic dependence of mechanical energy liberation on the eccentric force is seen in much more complex, multijoint movements. However, studies on vertical jumps preceded by drops from varied height have shown that the jump height is maximal when the drop height is within a limited range in untrained human subjects (4), suggesting the biphasic dependence of the kinetic energy liberation on the amount of negative work given to the muscle. Although this phenomenon has been interpreted in terms of the neuronal facilitation and depression occurring at the instant of countermovement (21), it may also be related to the intrinsic properties of muscle fibers. The present study investigated the interrelations between the eccentric force developed at the instant of countermovement, the mechanical power output during the following concentric action, and electrical activities of agonist and synergistic muscles in human squatting (knee, hip, and ankle extension) movements performed under an isotonic load. The results showed that the power output depends on the eccentric force in a biphasic manner that has no correlation with the electrical activities of the muscles involved in the movement.

METHODS

Subjects. Experiments were carried out with five male volunteers (ages 22–29 yr). They were well-trained athletes, because sufficient strength was required to overcome the large mechanical stress that was expected to act on muscles and connective tissues at the instant of countermovement. Table 1 shows the physical characteristics and strengths of the subjects in the squatting exercise. They were fully informed about the experimental procedure as well as the
Table 1. Physical characteristics of subjects

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1RM, one-repetition maximum weight with which subject can perform 1 repetition of exercise.

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purpose of the study, and their informed consent was obtained. This study was approved by the Ethics Committee for Human Experiments, University of Tokyo.

Measurements of ground reaction force. The subjects performed squatting exercises on a force plate (Kistler type 9281B, Kistler Instrument, Winterthur, Switzerland). The load used was a barbell weighing 50% of 1-repetition maximum (1RM; i.e., the maximal weight with which the subject can perform one action of exercise) for each subject (Table 1). The weight was placed just below the spinous process of the C7 vertebra. In the exercise without a countermovement (control), the subjects squatted at a knee angle of 90°, stayed still for 2–3 s, and then stood up to the upright position at their maximal effort (Fig. 1). The lowest hip position was recognized by the subjects correctly and reproducibly with the aid of a height-adjustable stool placed behind them. In the exercise with the countermovement, they squatted until their hip touched the stool, and at this moment, they reversed the motion as rapidly as possible to return to the upright position.

The rate of deceleration at the end of downward movement and the quickness of the subsequent reversal of motion were varied intensively ad libitum, to obtain varied level of eccentric force generated at the instance of countermovement. Before the measurements, the subjects practiced several times in movements to be examined with varied deceleration rate. For each subject, 5–10 measurements were made at intervals of 5 min. The force plate was connected to an electronic amplifier unit (Kistler type 5807, Kistler Instrument), and the output signals of the unit (the vertical and anteroposterior ground reaction forces) were sampled at 400 Hz by using a data-acquisition system (MacLab/8s, type ML780; AD Instruments Japan, Japan) and a personal computer (Performa 630, Macintosh).

Image analysis. The squatting movements were recorded by an autotracking video-recording system (OKK, Quick-Mag, Japan) at 30 frames/s (60 fields/s) from the left side in the sagittal plane. Markers were placed on the following anatomic landmarks on the left side to delimit the body segments: the top of greater trochanter, lateral epicondyle of the knee, the tip of lateral malleolus, and fifth metatarsal joint, as well as the left end of the barbell shaft. The coordinates for these markers were digitized automatically by Quick-Mag video-recording system and then low-pass filtered at 6 Hz. The output signals of the force plate and the video recordings were synchronized by simultaneously sending a trigger pulse to a video-recording system and data-acquisition system. The four-segment model was used to calculate the joint moments around the hip, knee, and ankle joints according to the link-segment model of Winter (25). The mass and the center of mass of each segment were based on the data of Dempster (7).

Recording of electromyographic (EMG) activity. EMG activities were recorded from vastus lateralis (VL), the long head of biceps femoris (BF) and the lateral head of gastrocnemius (GS) throughout the exercise movement. Bipolar surface electrodes (5 mm in diameter) were placed over the bellies of these muscles, with a constant interelectrode distance of 30 mm. The EMG signals were amplified, full-wave rectified, filtered through both low (time constant, 30 ms) and high (1-kHz) cut filters, converted from analog to digital, and finally stored in the computer.

Data analysis. Records of both ground reaction force and EMG signals were analyzed on the Macintosh Performa 630 computer. To obtain the vertical velocity of the center of mass (load plus body weight), changes in vertical force from that in the resting position were successively integrated with respect to time and then divided by the mass. The vertical velocity was also estimated as the velocity of the barbell shaft from the video images. The mechanical power output was calculated by multiplying the vertical component of force and the vertical velocity of center of mass. The rectified EMG signals were integrated with respect to time over the range of motion between the initiation of concentric action, when the vertical velocity of the center of mass was just zero, and the instant at which the maximal power was exerted (see Fig. 3). The obtained integrated EMGs (iEMGs) were averaged over time and used to evaluate the degree of motor-unit recruitment (2). These variables in the exercises with the countermovement were expressed relative to those in the exercises without the countermovement (control); in some measurements, their statistical significance was examined with Student’s paired t-test.

RESULTS

Changes in the ground reaction force. Typical changes in the ground reaction force and the vertical velocity of mass during squatting exercises are shown in Fig. 2. In exercises without the countermovement (control), the force stayed practically constant, at the level of load plus body weight, until it began to rise and caused an upward acceleration of mass (concentric action). Thus the force attained before the concentric action (Fp) was determined as the force just before its rising phase (Fig. 2A). Accordingly, the onset of upward movement was
slightly delayed from the time at which $F_0$ was measured.

In exercises with the countermovement (Fig. 2B), the force could be divided into three phases: 1) rapid decline in force, giving rise to a downward acceleration of mass; 2) counteracting rapid increase in force to decelerate the downward movement until it was stopped; and 3) subsequent, sustained increase in force to accelerate the upward movement of mass (positive velocity). Phases 1 and 2 represent the eccentric force because they appeared as the velocity was negative, whereas phase 3 represents the concentric force. In most cases, phase 2 exhibited a complicated configuration, in which a small peak of force appeared in the middle of the deceleration of the downward movement and was followed by a further, more gradual increase in force. We therefore determined $F_0$ as the force measured at the moment of the reversal of action, i.e., when the vertical velocity was zero. In both the exercises, with and without the countermovement, the force gradually increased as the load was lifted and then steeply declined due to the inertia of the load. Such a gradual increase in force is likely related to either length-dependent changes in the force-generating capacity of the muscle or to changes in the effective moment arm lengths around the knee and hip joints, because no consistent increase in EMG activities was observed with the gradual increase in force (Fig. 3).

Relations between the ground reaction force and the power output. Figure 4 shows a typical example of mechanical power obtained by multiplying the ground reaction force and the vertical velocity of mass. In most cases, the peak of power output practically coincided with that of force generation. As shown in the figure, the peak of power output was enhanced by a countermovement. However, it began to decrease when the maximal ground reaction force ($F_0$) attained before the concentric action exceeded a certain level. When the peak of positive power was plotted against $F_0$, both as values relative to those in control movements, it initially increased with the force up to the relative force level of $1.3-1.4F_0$, then decreased with the further

Fig. 2. Typical examples of changes in ground reaction force (solid lines) and vertical velocity of mass (dashed lines) during squatting exercises without (A) and with (B) countermovement. In exercise without countermovement (control), force reference ($F_0$) was determined as force just before its rising phase, whereas in exercise with countermovement, it was determined as force recorded at instant of reversal of direction of movement. For phases 1–3, see text.

Fig. 3. Typical examples of mechanical power obtained by multiplying ground reaction force and vertical velocity of mass (A) and electromyographic (EMG) signals recorded from vastus lateralis (VL; B) during squatting exercises with countermovement. ECC and CON, eccentric and concentric actions, respectively.
increase in force (Fig. 5A). The mean power output throughout the concentric phase showed a similar dependence on $F_0$ to that of the peak power (Fig. 6), suggesting that the ability of the muscle to generate power was enhanced throughout the concentric action. This is consistent with the absence of appreciable change in the time course of power generation with $F_0$ (Fig. 4).

Contributions of hip, knee, and ankle joints. Figure 5B shows relative torques around ankle, knee, and hip joints developed at the instant of maximal power output, each as a function of relative $F_0$. The knee-extension torque (●) increased with the eccentric force up to the relative force of 1.4 $F_0$, then decreased steeply with the further increase in force, whereas both the hip-extension and ankle-extension torques increased consistently with the eccentric force. Thus only the knee-extension torque exhibited the biphasic dependence on the eccentric force, which was similar to that of the power output (Fig. 5A). The absolute values of knee-, hip-, and ankle-extension torques at the peak of power output were 242.6 ± 21.4, 163.3 ± 18.0 and 93.9 ± 12.0 (mean ± SE) Nm, respectively. These observations strongly suggest that the power output in squatting exercise is primarily determined by the torque-generating capability of the knee extensors in the condition used in the present experiments, i.e., the maximal bend angle of the knee joint limited to within 90°.

iEMGs during movements. The EMG signals were recorded from a knee extensor (VL), a plantar flexor (GS), and a hip extensor (BF). In the EMG signals from VL, strong bursts were seen during the deceleration phase of the downward, eccentric action and just before the reversal of the motion, whereas relatively steady bursts followed during the subsequent concentric action, despite the steep increase in power output (Fig. 4B). The time-averaged iEMG (mean iEMG) was taken for the period of time between the onset of concentric action and the instant of maximal power generation. Although the iEMGs from all muscles examined tended to increase with the eccentric force, those at the relative force of 1.5 $F_0$ only showed statistically significant difference from those in the control movements. It should be noted that,
among the muscles examined, the iEMG from VL showed the least changes with the eccentric force, and even if it increased at the force of 1.5 $F_0$, both the knee-extension torque and the power output markedly declined at the same level of force (Fig. 5, A and B). For the hip extensor and planter flexor, it is still possible that the gradual increases in torque generation with the eccentric force are caused mainly by an elevation of their excitation level, i.e., additional fiber recruitment. As mentioned above, however, their role would be relatively minor in the present, prestretch-induced enhancement of power output in squatting exercises.

DISCUSSION

The present study shows that the capability of liberating mechanical power is improved by a counteraction in a representative multijoint exercise, the squat. The enhancement of power output is a function of the eccentric force developed before the load is lifted (concentric action) and increases with the force until the force reaches a certain limit. Thereafter, it decreases with the further increase in force. Such a biphasic dependence of the power output on the eccentric force is predominantly determined by the characteristics of knee extensors in the present experimental condition, because the knee-extension torque developed at the instant of the maximal power generation only exhibits a biphasic dependence on the eccentric force similar to that of the power output. This potentiation of torque generation in the knee extensors would not be primarily caused by an additional recruitment of motor units, because the time-averaged iEMG from VL was substantially unchanged with the eccentric force.

The present experiments were carried out with well-trained athletes because the generation of large eccentric force was thought to be dangerous for untrained subjects. In addition, some preliminary measurements with untrained subjects exhibited no reproducible enhancement in power output with the increase in $F_0$, suggesting that a certain level of skill for resistance-exercise training is required for obtaining consistent results. Such a limitation in subjects used may hinder generalization from the present results, because the long-term experience of the subjects in resistance training presumably affects the neuronal motor control of both eccentric and concentric actions. Collinader and Tesch (6) and Dudley et al. (9) have shown that resistance-exercise training, including intense eccentric muscular activities, causes an increase in the recruitment of motor units during maximal voluntary contractions. Probably because of such elevated nervous activity during and after the countermovements, maximal concentric actions were performed consistently, with steady level of muscular activities (see below). The joints and muscles involved in the squatting exercise are hip, knee, and ankle joints as well as their extensors. Which of these muscles is dominating in function (agonist) may depend on the style used in the exercise. In the present condition, the maximal bend angle of the knee joint was strictly limited at 90°, with the upper body slightly inclined forward (Fig. 1), so that the angular excursion during exercise around the knee joint was to be larger than those around the hip and knee joints. In this particular style, conventionally referred to as "half squat," hip and ankle extensors have been shown to play synergistic roles in the sense that their EMG activities relative to those in maximal voluntary contractions are much lower than that of the knee extensor (26). As the lowest hip position is lowered further ("deeper squat"), the relative contribution of the hip extensors increases. In the present experiments, every trial was made at the subject's maximal effort so that the activity of knee extensor, the agonist, was likely almost saturated, with little room for an additive effect of the stretch reflex (8, 15), and no substantial change was observed in the time-averaged iEMG except for transient bursts at the moment of the reversal of movement. By contrast, the gradual increases in EMG activities of both hip and knee extensors with the eccentric force may be related to an additional recruitment of motor units to submaximal contractions, which is caused by either stretch reflex or changes in motor-unit recruitment pattern. Recent studies have shown that motor units for fast-twitch fibers are predominantly recruited in submaximal eccentric contractions (11, 18). This would also affect the motor-unit recruitment pattern in the submaximal concentric contraction with a countermovement, because a larger number of fast-twitch fibers are already recruited during the preceding eccentric contraction. In elbow flexion, iEMG from elbow flexors has been shown to be unchanged when they are stretched at various rates during their maximal isometric contractions. In knee extension, on the other hand, iEMG from contracting knee extensors has even been shown to be depressed on stretch (23). The results of the present study of knee extensors are consistent with the studies of single-joint movements and suggest that the enhanced power output is mainly caused by an improvement of the capability of generating force, which is intrinsic in the muscle. In our companion report (22a), we have shown that the mechanical work production during elbow flexion performed in the isokinetic condition is enhanced by a ramp prestretch with varied velocities in a manner such that the amount of work liberated increases with
the eccentric force developed before the shortening of muscle until the eccentric force reaches \(~1.4\) maximal isometric force, then decreases with the further increase in force. In addition, contracting frog single fibers behave in a similar way against a ramp stretch followed by a ramp release, suggesting that a potentiation of force-generating capacity within the contractile machinery is involved in the stretch-induced enhancement of work production, as well as the reutilization of elastic energy stored in the SEC located in cross bridges (17) and tendons (13, 19, 20). The same mechanism can operate in the present squatting exercise, because both the overall power output of the body and the torque generated by knee extensors showed biphasic dependencies on the eccentric force, which are basically similar to that of the work production seen in the elbow flexion. However, comparison of the present study results with previous ones on elbow flexion requires caution, because the present measurements were made under nominally isotonic load, whereas the latter measurements were made in the isokinetic condition.

In the present study, the vertical components of both force and velocity changed with time (Fig. 2), although a constant (nominally isotonic) load was applied to the subjects. Consequently, none of the parameters related to the muscle contraction was fixed, and this makes a quantitative analysis extremely difficult. Under these circumstances, we used the maximal power output to compare the effect of countermovement, because it represents both the abilities of the muscle to exhibit steady-state velocity under a given load and to generate force rapidly to accelerate the mass, whereas the amount of work produced would be virtually unchanged regardless of the force and velocity attained during the movement. To compare the present results with our previous study on elbow flexion (22a), the relation between the mean power and \(F_0\) (shown in Fig. 6) is of particular importance. In isokinetic measurements made in the previous study, the work production is directly proportional to the mean power, because the work equals mean power \(\times\) time, where time is kept constant during isovelocity releases (90°/s) with a constant range of motion.

In the isokinetic condition where the range of movement is limited, the large eccentric force developed before the concentric action stretches the SEC to a greater extent so that it tends to diminish the distance of shortening of the contractile element (CE) during the following concentric action. It should be noted, therefore, that prestretching the muscle increases the storage of elastic energy in the SEC, which is proportional to the product of force and stretch distance, whereas it may reduce the work produced by the CE (1, 12). In the present experiments, on the other hand, the total elastic energy stored in the SEC should be retained as the concentric action proceeds, the ground reaction force gradually increases (Fig. 2B), and is released rapidly as the force begins to drop toward zero at the end of the movement. Thus, within certain limits, we speculate that the reutilization of the elastic energy stored in the SEC plays no major role in the present enhancement of power output. For more precise interpretation, the behaviors of SECS in every muscle involved should be separately taken into consideration. However, this is beyond the scope of the present study.

In a study of another multijoint movement (bench press), Wilson et al. (24) have shown the absence of positive correlation between musculotendinous stiffness and isokinetic, maximal eccentric force in well-trained athletes. They interpreted this to indicate that stiffer musculotendinous SEC has both advantageous and disadvantageous effects for the development of steady eccentric force. The stiffer SEC may effectively stretch the CE to a larger extent so that individual cross bridges develop larger force, whereas the SEC may readily overstretch the CE beyond its optimal length for force generation, or cause a “give” in interacting cross bridges (14). This implies that the mechanical enhancement of concentric contraction subsequent to a countermovement depends on both the stretch distance of SEC and the degree of potentiation in the CE during the eccentric action. Such a mechanism may operate in the present, biphasic dependence of power on the peak of eccentric force, because the apparent stiffness of SEC may change with the velocity of stretch depending on the viscous component included.

When a frog single fiber is stretched for a short distance and then kept at the stretched length during the plateau phase of an isometric contraction, it maintains the force higher than that developed without stretch (10). Releasing it from the stretched state under a given isotonic load gives rise to an elevation of steady-state shortening velocity, which leads to an upward shift of the force-velocity and force-power relationships (22). Such phenomena have been interpreted in terms of the potentiation of force-generating capability at the level of either cross-bridge interactions or intracellular regulatory processes, although no convincing theory has so far been put forward. The present study suggests that the similar stretch-induced potentiation of the force-generating capability of muscle fibers plays a part in the countermovement-induced enhancement of power output in human multijoint exercises where dominating single-joint movement exists. The presence of an optimal eccentric force for potentiating the intrinsic ability of muscle fibers to exert mechanical power implies that particular attention should be paid to the rate of deceleration during the eccentric action to gain the highest performance in a variety of exercises with the countermovement.

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