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Interplay among the changes of muscle strength, cross-sectional area and maximal explosive power: theory and facts

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Abstract A model has recently been proposed to predict the changes of mechanical power (\dot{W}) during a maximal explosive effort (such as a standing high jump off both feet) following an adaptation (e.g. training/de-training). The model is based on the assumption that, all other things being equal (*ceteris paribus*), the predicted changes in \dot{W} depend on the measured changes of muscle force (F) or cross-sectional area (CSA) only. It follows that, if the measured changes in \dot{W} are not equal to those predicted by the model, factors other than a change in F (or CSA) must be responsible for this difference. The model does not allow the determination of factors specifically involved in the adaptation process but it helps in discriminating whether an adaptation has taken place at a local level (when the observed changes in F would be attributed to factors other than the observed changes in CSA, e.g. co-contractions, fibre type modifications...), or at a central level (when the observed changes in \dot{W} would be attributed to other factors than the observed changes in F , e.g. co-ordination of multiple joints and muscle groups...), or in both regions. In this paper the model has been applied to data reported in the literature on disuse (BR, bed rest), de-conditioning (SF, space flight), strength training (ST) and de-training (DT). The results of these calculations have confirmed previous observations on the determinants of the adaptation process and further suggest: (1) that training for one specific motor task (e.g. ST) could affect the performance of a second task (e.g. a maximal explosive jump) but that, as soon as

the trained motor task is terminated (DT), this ability is re-gained; and (2) that neuromuscular *impairment* in disuse (BR) is closer to de-training than to the de-conditioning brought about by weightlessness (SF).

Keywords Maximal explosive power · Cross-sectional area · Disuse · De-conditioning · Training

Abbreviations

- \dot{W} : Maximal explosive power
- \dot{W}_{pre} : \dot{W} before adaptation
- \dot{W}_{post} : \dot{W} after adaptation
- \dot{W}_{ch} : $\dot{W}_{post} / \dot{W}_{pre}$
- F : Force (either F_{iso} or F_{use} , see below)
- F_{pre} : F before adaptation
- F_{post} : F after adaptation
- F_{ch} : F_{post} / F_{pre}
- CSA: Cross-sectional area
- CSA_{pre} : CSA before adaptation
- CSA_{post} : CSA after adaptation
- CSA_{ch} : CSA_{post} / CSA_{pre}
- $k_{a,ch}$: $F_{iso,ch} / CSA_{ch}$
- $k_{c,ch}$: $\dot{W}_{ch} / F_{iso,ch}$
- $k_{ac,ch}$: \dot{W}_{ch} / CSA_{ch} (and also: $k_{a,ch} k_{c,ch}$)
- F_{iso} : Maximal isometric force
- F_p : Peak (maximal) force during the jump
- F_{use} : Force available during the jump
- T : Maximal isometric torque
- \dot{s} : Speed
- \dot{s}_{ch} : $\dot{s}_{post} / \dot{s}_{pre}$
- n : F_{iso} / mg (mg = body weight)
- α : Angle between the vertical and the direction of the movement

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Introduction

In a recent paper Minetti (2002) proposed a model for predicting the changes of mechanical power (during a maximal explosive effort, such as a standing high jump

off both feet) brought about by changes of muscle cross-sectional area or isometric force. The model is based on the assumption that, all other things being equal (*ceteris paribus*), the changes of mechanical power depend on the changes of muscle force (or cross-sectional area) only. The model shows that if, as an example, the isometric force (F_{iso}) decreases by 30% ($F_{iso,post}/F_{iso,pre} = F_{iso,ch} = 0.7$) the explosive power (\dot{W}) decreases to a larger extent (by 50%: $\dot{W}_{post}/\dot{W}_{pre} = \dot{W}_{ch} = 0.5$) and hence that a $\dot{W}_{ch}/F_{iso,ch}$ ratio $\neq 1$ (~ 0.7 in this case) should be expected even when the force is the only factor known to be affected by the adaptation process.

The interplay between \dot{W}_{ch} and $F_{iso,ch}$ has often been misinterpreted since a $\dot{W}_{ch}/F_{iso,ch}$ ratio lower than 1 has been assumed to indicate an impairment in motor control (which is not necessarily the case, as demonstrated above). The misunderstanding has arisen because this ratio was *utilized and interpreted* in analogy with the more commonly determined ratio between isometric force changes ($F_{iso,ch}$) and changes of cross-sectional area (CSA_{ch}). In this latter case a change in force not proportional to the change in CSA (a $F_{iso,ch}/CSA_{ch}$ ratio $\neq 1$) is indeed taken as indicative of the influence of factors other than CSA in the development of force (see below for a more detailed discussion on this point). On the contrary, as shown by Minetti (2002) and mentioned above, this is not the case for the $\dot{W}_{ch}/F_{iso,ch}$ ratio since power and force changes are not linearly related.

The reasons underlying the state of affairs summarized above are described in depth in the paper of Minetti (2002) to which the reader is referred for further detail. Suffice it to say here that the model assumes that the leg extensors muscles act, before and after adaptation, against the same load (e.g. the body weight), over the same distance (s) (e.g. in a squat jump they extend the knee angle from 90° to 180°) and with a force which is constant in time (e.g. that is independent of the speed of shortening). Force is given by the product of mass and acceleration and hence, for a given mass (when a constant body weight is assumed), the change in force before and after adaptation (F_{ch}) is the only determinant (*ceteris paribus*) of the corresponding change in acceleration, from which the speed (\dot{s}) can be derived by integration. Since power is given by the product of force and speed, the change in force before and after adaptation is still the only determinant (*ceteris paribus*) of the corresponding change in power ($\dot{W}_{ch} = \dot{W}_{post}/\dot{W}_{pre}$). As pointed out by Minetti (2002) this line of reasoning holds if and only if the change in force is indeed “the only” determinant of the change of \dot{s} or \dot{W} (*ceteris paribus*: all other things being equal). As indicated by Minetti (2002) the exponents to which the force changes have to be raised to predict the duration, final speed and power of the maximal extension are -0.5, 0.5 and 1.5 respectively. The model takes into consideration also the effects of gravity (g) so that it can be applied to predict the changes in \dot{W} , Δt and \dot{s} on the basis of observed (measured) changes in F in different experimental con-

ditions: from vertical jumps to bench press exercises and jumps on a sledge ergometer.

The model allows one to estimate the occurrence and relative importance of different factors involved in the adaptation process. Indeed, the model predicts:

1. The changes in power to be expected on the basis of the changes in force; but also
2. The changes in power to be expected on the basis of the changes in cross-sectional area (CSA, assumed to be proportional to F) *ceteris paribus*. In the first case, if the measured values of \dot{W}_{ch} ($= \dot{W}_{post}/\dot{W}_{pre}$) and F_{ch} ($= F_{post}/F_{pre}$) yield a \dot{W}_{ch}/F_{ch} ratio different to that predicted by the model, it can legitimately be inferred that factors other than F_{ch} must be responsible for the differences between the predicted and observed values of \dot{W}_{ch} . Similarly, in the second case, a discrepancy between the predicted and measured \dot{W}_{mch}/CSA_{ch} ratios suggests that factors other than CSA_{ch} ($= CSA_{post}/CSA_{pre}$) were responsible for the differences between the predicted and observed values of \dot{W}_{ch} . This model, therefore, represents an interesting tool for evaluating the determinants of the changes of muscular power observed after immobilisation or weightlessness, strength or explosive training, as well as after detraining.

Approach to the problem

The calculations proposed by Minetti (2002), when combined with the observed changes of mechanical power (\dot{W}_{ch}) maximal isometric force ($F_{iso,ch}$) and cross-sectional area (CSA_{ch}), allow one to obtain the changes of two constants (see Fig. 1) relating:

1. CSA to muscle force ($k_{a,ch}$) and
2. Muscle force to actual power output ($k_{c,ch}$).

The values of these constants and of their product ($k_{ac,ch} = k_{c,ch} \cdot k_{a,ch}$) indicate whether or not the “*ceteris paribus* hypothesis” holds, as summarized below.

- Hypothesis 1 ($k_{a,ch}$): $F_{iso,ch}$ is due to CSA_{ch} only: $F_{iso,ch}/CSA_{ch} = 1$ ($k_{a,ch} = 1$). If: $F_{iso,ch}/CSA_{ch} \neq 1$ ($k_{a,ch} \neq 1$) then factors in addition to CSA_{ch} determine the further change in $F_{iso,ch}$.
- Hypothesis 2 ($k_{c,ch}$): \dot{W}_{ch} is due to $F_{iso,ch}$ only: $\dot{W}_{ch}/F_{iso,ch}$ measured = $\dot{W}_{ch}/F_{iso,ch}$ predicted ($k_{c,ch} = 1$). If $\dot{W}_{ch}/F_{iso,ch}$ measured $\neq \dot{W}_{ch}/F_{iso,ch}$ predicted ($k_{c,ch} \neq 1$) then factors in addition to $F_{iso,ch}$ determine the further change in \dot{W}_{ch} .
- Hypothesis 3 ($k_{ac,ch}$): \dot{W}_{ch} is due to CSA_{ch} only: \dot{W}_{ch}/CSA_{ch} measured = \dot{W}_{ch}/CSA_{ch} predicted ($k_{ac,ch} = 1$). If \dot{W}_{ch}/CSA_{ch} measured $\neq \dot{W}_{mch}/CSA_{ch}$ predicted ($k_{ac,ch} \neq 1$) then factors in addition to CSA_{ch} determine the further change in \dot{W}_{ch} .

The determination of $k_{a,ch}$ ($F_{iso,ch}/CSA_{ch}$) has been used extensively to investigate whether neuro-mechanical/neuro-muscular factors are involved in the training/

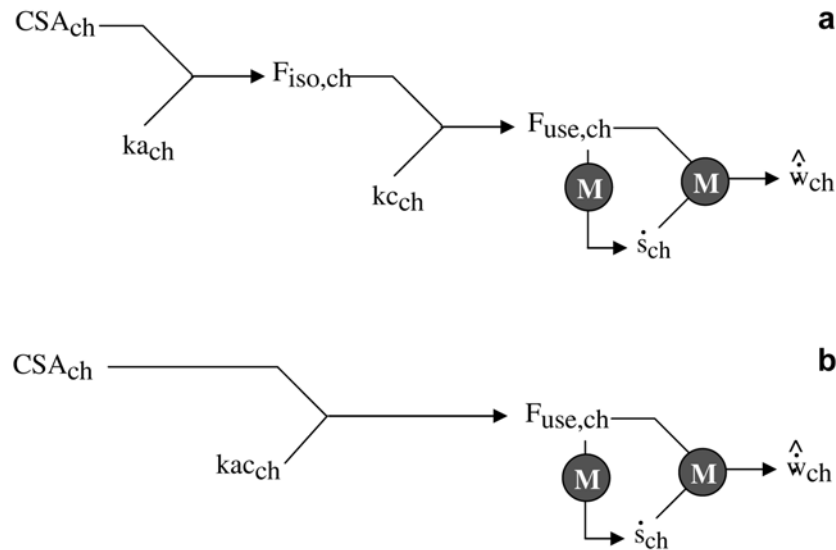


Fig. 1 As indicated by Minetti (2002), the chain of events leading from muscle cross-sectional area changes (CSA_{ch}) to changes in power output (\dot{W}_{ch}) can be split into two main conceptual steps (diagram A). The first one leads from CSA_{ch} to isometric force changes ($F_{iso,ch}$), the second one from $F_{iso,ch}$ to power changes (\dot{W}_{ch}) (or to speed changes: \dot{s}_{ch}). If these quantities are measured before and after a training/detraining process, the model (M) proposed by Minetti (2002) allows one to calculate the post to pre ratios of two constants: (1) $k_{a,ch} (= F_{iso,ch}/CSA_{ch})$, expressing the contribution of *neuro-muscular/local factors* (e.g. muscle mass and architecture, recruitment pattern, fibre type, co-contractions...); and (2) $k_{c,ch} (= \dot{W}_{ch}/F_{iso,ch})$, expressing the contribution of *neural/central factors* (e.g. co-ordination of multiple joints and muscle groups, specificity of motor task...). As indicated in diagram B, a further step leads directly from CSA changes to power (or speed) changes ($k_{acm,ch} = \dot{W}_{ch}/CSA_{ch}$). Adapted from Minetti (2002), see text for details

detraining process. Indeed a $k_{a,ch}$ value equal to 1 is generally taken as an indication: that no changes in specific tension have occurred; and hence that all the observed changes in force have to be attributed to changes in CSA.

On the other hand, a $k_{a,ch}$ higher or lower than 1 is generally taken as an indication that factors other than CSA have contributed to the observed changes in force. Among these factors are changes in muscle architecture (e.g. Kawakami et al. 1993), fibre type modifications, changes in the agonist/antagonist activation pattern (e.g. Häkkinen et al. 1998) as well as changes in the recruitment pattern and/or in the neural drive (as indicated by changes in the F_{iso}/EMG ratio, e.g. Moritani and De Vries 1980), just to name a few.

A smaller number of studies have reported, in addition to data on F_{iso} and CSA, data on maximal explosive power. In analogy with the changes of force, the changes in power output observed after adaptation could be attributed: (1) to changes in CSA only or (2) to several other factors. In addition to the factors listed above (which determine the changes of F_{iso} above those of CSA), the additional changes in power output after adaptation could be related to changes in the co-ordination of multiple joints/muscle groups, to the specificity of the motor task (Jones et al. 1989; Dudley et al. 1991) and, again, to

an improved pattern of activation of the agonists-antagonists muscles involved in the specific task.

To summarize, in general terms, a $k_{a,ch} \neq 1$ indicates the occurrence of *local adaptation* whereas a $k_{c,ch} \neq 1$ indicates the occurrence of *central adaptation*. Therefore, whereas the model does not allow the distinguishing among the specific factors known to affect the adaptation process, it can be used to investigate the *level* at which the adaptation has taken place.

Aim of the study

The intention of this paper was to re-evaluate some data reported in the literature to enable the estimation of the contribution of local and central factors to the adaptation process. To achieve this aim, the model proposed by Minetti (2002) was applied to data obtained after disuse (bed rest, BR: Ferretti et al. 2001), de-training (after strength training, DT: Häkkinen et al. 1998, 2000) and de-conditioning (space flight, SF: Antonutto et al. 1998, 1999) as well as after strength training (ST) (Häkkinen et al. 1981, 1998, 2000; Izquierdo et al. 2001, Ferri, personal communication), explosive training (ET) (Paavolainen et al. 1991) or general training (GT) (De Vito et al. 1999). Even if these studies represent only a relatively small sample of the literature on training and de-training, disuse and de-conditioning they were selected because they report changes of mechanical explosive power together with changes of cross-sectional area and maximal isometric force, i.e. all the variables required by the model. These studies, therefore, provided us with the necessary values for our calculations or, alternatively, reported data from which these values could be derived/estimated as described below.

Calculations

As shown by Minetti (2002), the changes in explosive power (\dot{W}_{ch}) following muscle conditioning can be

calculated on the basis of the changes in the force available during the jump ($F_{\text{use, ch}}$) according to:

$$\dot{W}_{\text{ch}} = F_{\text{use, ch}} \left(\frac{nF_{\text{use, ch}} - \cos \alpha}{n - \cos \alpha} \right)^{\frac{1}{2}} \quad (1)$$

where n is the ratio between the maximal isometric strength of the active muscles and the force necessary to sustain vertically the body weight ($n = F_{\text{iso}}/mg$, m being the body mass) and α is the angle between the vertical and the direction of the movement. For jumps on a sledge ergometer inclined at 20° with the horizontal (as was the case for all the SF data considered in this study) $\alpha = 70^\circ$, for horizontal leg extension (such as bench press) $\alpha = 90^\circ$, for vertical jumps (e.g. squat jumps) $\alpha = 0^\circ$.

The term F_{use} is the input to the model and indicates the force available during the jump; as indicated above, this force is assumed to be constant in time and load independent. The changes in F_{use} do not necessarily mirror the changes in isometric force ($F_{\text{iso, ch}}$) even if the two are sequentially related. Indeed, as schematically shown in Fig. 1, the chain of events leading from CSA changes to changes in power output can be split into two main conceptual steps (diagram A). The first one leads from CSA (CSA_{ch}) to isometric force ($F_{\text{iso, ch}}$), the second one from $F_{\text{iso, ch}}$ to actual force available during the jump ($F_{\text{use, ch}}$). A further step (diagram B), described by Eq. 1 or Eq. 6 (see below), leads from actual force changes ($F_{\text{use, ch}}$) to power changes (\dot{W}_{ch} ; Eq. 1) or to speed changes (\dot{s}_{ch} , Eq. 6). The steps described above can be expressed algebraically as follows:

$$F_{\text{iso, ch}} = \text{CSA}_{\text{ch}} \cdot k_{\text{a, ch}} \quad (2)$$

$$F_{\text{use, ch}} = F_{\text{iso, ch}} \cdot k_{\text{c, ch}} \quad (3)$$

$$F_{\text{use, ch}} = \text{CSA}_{\text{ch}} \cdot k_{\text{ac, ch}} \quad (4)$$

where the constants $k_{\text{a, ch}}$, $k_{\text{c, ch}}$ and $k_{\text{ac, ch}}$ relate the appropriate variables and the subscript ch indicates that we are dealing with post to pre ratios. Obviously enough: $k_{\text{ac, ch}} = k_{\text{a, ch}} \cdot k_{\text{c, ch}}$.

The term $k_{\text{a, ch}}$ can be calculated from the ratio $F_{\text{iso, ch}}/\text{CSA}_{\text{ch}}$ (both experimentally measured); of the three hypothesis reported at the beginning of the theory section, hypothesis 1 can therefore be tested rather easily. Hypothesis 2 (i.e. that the observed changes in power have to be attributed to changes in force only) can be tested combining Eq. 1 and Eq. 3 on the basis of the measured values of $F_{\text{iso, ch}}$ and \dot{W}_{ch} . Indeed, if $k_{\text{c, ch}} = 1$ it also follows that $F_{\text{iso, ch}} = F_{\text{use, ch}}$. If this is so the hypothesis is true and no other factors in addition to F_{iso} are required to explain the observed changes in power output. Hypothesis 3 (i.e. that the observed changes in power have to be attributed to changes in CSA only) can be tested by combining Eq. 1 and Eq. 4 on the basis of the measured values of CSA_{ch} and \dot{W}_{ch} . Indeed, if $k_{\text{ac, ch}} = 1$ it also follows that $\text{CSA}_{\text{ch}} = F_{\text{use, ch}}$. If this is so,

the hypothesis is true and no other factors in addition to CSA are needed to explain the observed changes in power output.

Hence, in order to test the hypotheses put forth by the model, the following data are required:

1. The measured post to pre ratios of explosive power ($\dot{W}_{\text{ch}} = \dot{W}_{\text{post}}/\dot{W}_{\text{pre}}$);
2. The measured post to pre ratios of isometric force ($F_{\text{iso, ch}} = F_{\text{iso, post}}/F_{\text{iso, pre}}$);
3. The measured post to pre ratios of cross-sectional area ($\text{CSA}_{\text{ch}} = \text{CSA}_{\text{post}}/\text{CSA}_{\text{pre}}$); in addition to the values of
4. n and
5. α .

The equations resulting from the combination of Eq. 1 and Eq. 3 or Eq. 1 and 4 are incomplete 3rd-order polynomials, their solution is given by Minetti (2002).

When investigating the effects of training/de-training on the maximal explosive power of the lower limbs, the differences in the height of the jump (h_{max}) are often reported instead of the differences in power output. Assuming the same take off and landing postures, the maximal speed at take off (\dot{s}_{max}) can be calculated from the height of the jump:

$$\dot{s}_{\text{max}} = \sqrt{2gh_{\text{max}}} \quad (5)$$

In turn, since, according to Minetti (2002) the velocity changes depend on the force changes, as described by:

$$\dot{s}_{\text{ch}} = \left(\frac{nF_{\text{use, ch}} - \cos \alpha}{n - \cos \alpha} \right)^{\frac{1}{2}} \quad (6)$$

the constants $k_{\text{c, ch}}$ and $k_{\text{ac, ch}}$ can also be computed by combining Eq. 2 and Eq. 3 with Eq. 6 (instead of Eq. 1), see also Fig. 1.

The maximal isometric strength of the knee extensor muscles (F_{iso}) was not measured in some of these studies. In these cases we have proceeded as follows:

1. In the studies in which the maximal isometric torque (T) was assessed, the changes of the post to pre values of torque (T_{ch}) have been taken as an estimate of the changes of isometric force ($F_{\text{iso, ch}}$), since the effects of the lever arm cancel out
2. In the studies in which the peak dynamic force (F_{p} , as attained during the jump itself) was the only force index reported, we calculated $F_{\text{iso, ch}}$ assuming that peak dynamic force was about half of that developed isometrically (hence $F_{\text{iso, ch}} = 2 F_{\text{p, ch}}$). The rationale on which this last assumption is based is described in the Appendix.

Finally, $n (= F_{\text{iso}}/mg)$ was assumed to be equal to 2.5 in all cases (as proposed by Minetti 2002) even if the data we gathered from the literature referred to subjects who would be characterized presumably by different values of n (from young athletes to elderly people). The

rationale on which this last assumption was based is also described in the Appendix.

Results

Table 1 (Disuse) and Table 2 (Training) give the post-to-pre ratios of cross-sectional area ($CSA_{ch} = CSA_{post}/CSA_{pre}$), isometric force ($F_{iso,ch} = F_{iso,post}/F_{iso,pre}$) and maximal explosive power ($\dot{W}_{ch} = \dot{W}_{post}/\dot{W}_{pre}$) as obtained from the literature. The post to pre ratios of maximal speed ($\dot{s}_{ch} = \dot{s}_{post}/\dot{s}_{pre}$) are reported instead of \dot{W}_{ch} for those cases where the performance index is the height of the jump. The predicted values of \dot{W}_{ch} obtained from Eq. 1 by substituting CSA_{ch} for $F_{use,ch}$ represent the change of power output that could be attributed to the changes of CSA only. Hence, the difference between the measured and predicted values of \dot{W}_{ch} is an indication of the overall effect of neural factors (both *local* and *central*) on power output after training or de-training, disuse or de-conditioning. A more precise evaluation of the contribution of the changes of neural and muscular factors on the power output changes is obtained by computing the values of $k_{a,ch}$, $k_{c,ch}$ and $k_{ac,ch}$ from the measured/calculated values of \dot{W}_{ch} , $F_{iso,ch}$ and CSA_{ch} . The values of $k_{a,ch}$, $k_{c,ch}$ and $k_{ac,ch}$ are given in Tables 1 and 2 and in Fig. 2; in the figure the values are averages obtained from one or more studies (bars represent one standard deviation): ET, explosive training (Paavolainen et al. 1991); GT, general training (De Vito et al. 1999); ST, strength training (Häkkinen et al. 1981, 1998, 2000;

Izquierdo et al. 2001; Ferri, personal communication); DT, detraining after strength training (Häkkinen et al. 1998, 2000); BR, bed rest (Ferretti et al. 2001); SF, space flight (Antonutto et al. 1998, 1999).

Discussion

Critique of the model

The few lines that follow are devoted to a brief discussion of the main assumptions on which the model is based. The model assumes that:

1. No changes in load (body mass) occurred after adaptation. Even if changes in body mass are a common finding after training/detraining, the post to pre differences in load can be considered negligible (e.g. differences of 1 kg compared to 75 kg of body mass after 42 days of bed rest, Ferretti et al. 2001), so the assumption of a constant load appears reasonable. The model also assumes that
2. The force generated by the leg extensors is constant in time; this assumption does not correspond to *real* conditions since the force generated by the muscles changes as a function of time and of the speed of shortening. Nevertheless we think this assumption to be reasonable, as a first approximation, since in all cases we are dealing with post to pre ratios of power rather than with absolute values.

Table 1 Ratios of changes (post-to-pre values) of cross-sectional area (CSA_{ch}), peak force (F_{ch}), peak velocity (\dot{s}_{ch}) and peak power (\dot{W}_{ch}) as measured before and after space flight, bed rest and detraining (after strength training). The predicted values of peak power (\dot{W}_{ch}) and the ratios of the three constants relating F_{ch} and CSA_{ch} to \dot{W}_{ch} are reported as well. See text for details. Data obtained from the following references: (1) Antonutto et al. personal communication, (2) Antonutto et al. (1998), (3) Antonutto et al. (1999), (4) Ferretti et al. (2001), (5) Häkkinen et al. (1981), (6) Häkkinen et al. (2000). The cross-sectional area (CSA) of the thigh

was estimated by means of nuclear magnetic resonance (*MRI*), ultrasonic scanner (*US*) computed tomography (*CT*) or by measures of thigh girth (*TG*). In (3) the measured CSA was the one of the calf, its % change after SF was shown to be the similar to that observed by measures of *TG* (see (3) for a detailed discussion). Only in (4) and (6) the measured CSA was the one of the leg extensors only (*ext*). Maximal explosive power was assessed during vertical jumps started from a squatting position (*SJ*) in (4), (5) and (6); on a sledge apparatus (inclined of 20° in respect to the horizontal) in (1), (2) and (3)

Disuse	<i>n</i>	Age (years)	CSA	CSA_{ch} measured	$F_{iso,ch}$ measured	\dot{s}_{ch} measured	\dot{W}_{ch} measured	\dot{W}_{ch} predicted	$k_{a,ch}$	$k_{c,ch}$	$k_{ac,ch}$
Space flight											
180 days (1)	1	40	TG	0.819	0.816 ^a		0.671	0.715	0.996 ^a	0.956 ^a	0.952
379 days (1)	1	42	TG	0.834	0.656 ^a		0.421	0.738	0.787 ^a	0.895 ^a	0.704
21 days (2)	1	40	TG	0.867	0.644 ^a		0.535	0.788	0.742 ^a	1.054 ^a	0.783
31 days (3)	1	53	MRI ^d	0.910	0.870 ^a		0.694	0.854	0.956 ^a	0.915 ^a	0.875
169 days (3)	1	47	MRI ^d	0.940	0.736 ^a		0.540	0.902	0.783 ^a	0.927 ^a	0.726
180 days (3)	1	37	MRI ^d	0.870	0.687 ^a		0.409	0.792	0.789 ^a	0.841 ^a	0.664
180 days (3)	1	39	MRI ^d	0.800	0.730 ^a		0.535	0.687	0.913 ^a	0.929 ^a	0.848
Bed rest											
42 days (4)	7	28	MRI ext	0.883	0.742 ^{b,c}		0.760	0.756	0.840	1.163	0.977
De-training											
8 weeks (5)	14	26	TG	0.994	0.880	0.986		0.987	0.885	1.117	0.989
24 weeks (6)	7	41	US ext	0.905	0.872 ^b	0.981		0.801	0.964	1.120	1.079
24 weeks (6)	7	69	US ext	0.885	0.905 ^b	0.979		0.760	1.023	1.077	1.102

^aData calculated on the basis of the peak force values as measured during the jump (see text and Appendix)

^bData refer to maximal isometric torque (and not to F_{iso})

^cData from Berg et al. (1997)

^dData from Zange et al. (1997). *n* number of subjects

Table 2 Ratios of changes (post-to-pre values) of cross-sectional area (CSA_{ch}), peak force (F_{ch}), peak velocity (\dot{s}_{ch}) and peak power (\dot{W}_{ch}) as measured before and after strength training, general training and explosive training. The predicted values of peak power (\dot{W}_{ch}) and the ratios of the three constants relating F_{ch} and CSA_{ch} to \dot{W}_{ch} are also reported. See text for details. Data obtained from the following references: (7) De Vito et al. (1999), (8) Häkkinen et al. (1998), (5) Häkkinen et al. (1981), (6) Häkkinen et al. (2000), (9)

Training	n	Age (years)	CSA	CSA_{ch} measured	$F_{iso,ch}$ measured	\dot{s}_{ch} measured	\dot{W}_{ch} measured	\dot{W}_{ch} predicted	$k_{a,ch}$	$k_{c,ch}$	$k_{ac,ch}$
General training											
12 weeks (7)	11	63	US ext	1.015	1.200 ^a		1.280	1.033	1.182 ^a	0.954 ^a	1.127
Strength training											
24 weeks (8)	11	72	US ext	1.021	1.372	1.054		1.045	1.344	0.778	1.045
24 weeks (8)	10	67	US ext	1.056	1.524	1.049		1.124	1.442	0.696	1.004
24 weeks (8)	10	42	US ext	1.054	1.351	1.031		1.120	1.281	0.769	0.985
24 weeks (8)	11	39	US ext	1.093	1.637	1.076		1.208	1.498	0.669	1.001
16 weeks (5)	14	26	TG	1.012	1.211	1.047		1.026	1.196	0.874	1.045
16 weeks (9)	8	67	MRI ext	1.073	1.171 ^b	1.025		1.162	1.092	0.880	0.961
24 weeks (6)	12	41	US ext	1.095	1.214 ^b	1.035		1.212	1.109	0.859	0.953
24 weeks (6)	10	70	US ext	1.067	1.214 ^b	1.061		1.148	1.138	0.885	1.008
24 weeks (6)	7	41	US ext	1.080	1.270 ^b	1.041		1.177	1.177	0.827	0.973
24 weeks (6)	7	69	US ext	1.040	1.333 ^b	1.095		1.088	1.282	0.840	1.077
16 weeks (10)	11	46	US ext	1.133	1.290		1.474	1.205	1.139	1.001	1.140
16 weeks (10)	11	64	US ext	1.113	1.250		1.250	1.174	1.123	0.925	1.039
Explosive training											
6 weeks (11)	7	20	TG	0.982	0.959	1.055		0.962	0.976	1.114	1.087

^aData calculated on the basis of the peak force values as measured during the jump (see text and Appendix); n number of subjects

^bData refer to maximal isometric torque (and not to F_{iso})

Finally, a criticism of the methods is that, since the experimental data used as an input to the model were obtained from different test protocols which employed different measuring devices (e.g. CSA in some papers was obtained from measures of thigh girth), the variability of the values of interest may have affected the results and hence the accuracy of the predictions.

Nevertheless, in spite of the non-homogeneity of the data and of the coarse definition of *local* ($k_{a,ch}$) and *central* ($k_{c,ch}$) influences on the variables investigated, the picture emerging from these calculations confirms and extends the observations reported in the literature about the determinants of the adaptation process, as will be discussed below.

Training and de-training

The constant $k_{a,ch}$ is analogous to the “specific tension” which is calculated from the F/CSA ratio; specific tension is generally increased after training and decreased after de-training and disuse (Enoka 1994; Milesi et al. 2000). Following a system *perturbation/adaptation* the mechanisms which could be responsible for the changes in specific tension are peripheral (such as the fibre type composition and the fibre architecture) as well as neural (such as reflex excitability and motor unit recruitment pattern) (e. g. Jones et al. 1989; Enoka 1997). By analogy with the changes in specific tension, $k_{a,ch}$ (obtained from the $F_{iso,ch}/CSA_{ch}$ ratio) can be expected to be greater than 1 after training and to be less than 1 after de-training/de-conditioning.

Ferri, personal communication, (10) Izquierdo et al. (2001), (11) Paavolainen et al. (1991). Cross-sectional area was measured (at the thigh level in all cases) using: ultrasound scanners (*US*), nuclear magnetic resonance (*MRI*), or by measures of thigh girth (*TG*). In all but TG cases the CSA refers to the leg extensors only. Maximal explosive power was assessed during vertical jumps started from a squatting position (*SJ*) in all cases but in (10) (bench press)

As shown in Tables 1 and 2 and in Fig. 2, in DT, BR and SF the decrease of CSA was smaller than the observed decrease of F_{iso} so that $k_{a,ch}$ turned out to be less than 1 in these three conditions. On the other hand, the increase of CSA was smaller than the observed increase of F_{iso} so that $k_{a,ch}$ turned out to be greater than 1 in ST and GT. Even if $k_{a,ch}$ turned out to be less than 1 in explosive training (ET), Paavolainen and coworkers reported that both F_{iso} and CSA were not significantly changed after explosive training and hence the change in $k_{a,ch}$ probably does not reach a significant level either. After explosive training $k_{c,ch}$ was found to be greater than 1 indicating that this type of training was indeed useful in improving the co-ordination of multiple joints/muscle groups in this specific motor task (a maximal two legs jump). On the contrary, the constant $k_{c,ch}$ was found to be less than 1 after general (GT) and strength training (ST).

Training adaptations depend on the task, the muscle length and the muscle velocity used for training (e.g. Jones et al. 1989; Dudley et al. 1991). Moreover, adaptations are observed not only in the trained muscle group but also in all the muscles needed to stabilize that particular limb (as well as the rest of the body) and even in the homologous contra-lateral muscle groups (e.g. Enoka 1994). It was therefore expected that some differences in $k_{c,ch}$ would be observed among different training protocols: the more different the trained task from a dynamic two legs explosive jump the lower the value of $k_{c,ch}$. The data reported in Fig. 2 and in Tables 1 and 2 suggest that not only is the adaptation task dependent but also that training for a specific motor task could have detrimental effects on the motor control of muscle groups different from the ones

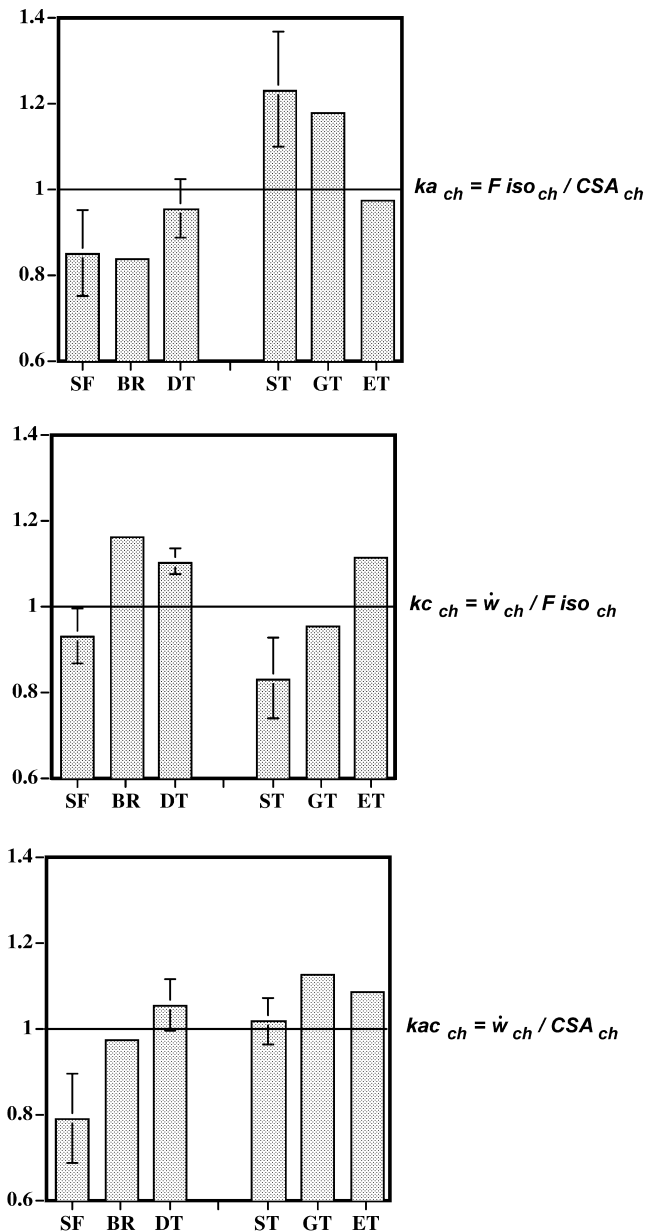


Fig. 2 Average values of $k_{a, ch}$, $k_{c, ch}$ and $k_{ac, ch}$ as calculated from the data reported in Tables 1 and 2 (bars represent one standard deviation): *ET* Explosive training, *GT* general training, *ST* strength training, *DT* detraining after strength training, *BR* bed rest, *SF* space flight, where *ch* indicates the post to pre ratio of the appropriate quantities

that have been specifically trained. This suggestion seems to be supported by the finding that $k_{c, ch}$ is greater than 1 following detraining (DT) suggesting that, as soon as the specific motor task is terminated (strength training in this case), other motor pathways are (possibly) less inhibited and could improve without any specific *re-training*.

The observation that $k_{c, ch}$ is greater than 1 after disuse and less than 1 after training (ST and GT) also reflects the finding that skeletal muscle response to decreased use is characterized by a conversion of slow to

fast muscle fibre types, whereas muscles respond to an increased use by becoming “slower” (fast to slow fibre type transformation, for a review see Lieber 1992).

The constant $k_{ac, ch}$ can be simply calculated as the product of $k_{a, ch}$ and $k_{c, ch}$ and is a combination of both *local* and *central* factors in the development of maximal power output; $k_{ac, ch}$ was found to be lower than 1 after BR and SF and greater than 1 in all other cases.

The data reported in Fig. 2 for ST are average values as obtained from studies in which not only the training protocol was different but also its duration as well as the age, sex and training status of the subjects. All these factors affect in different ways the adaptation process and this is indicated by the large standard deviation reported in the figure. Nevertheless, in all the ST studies:

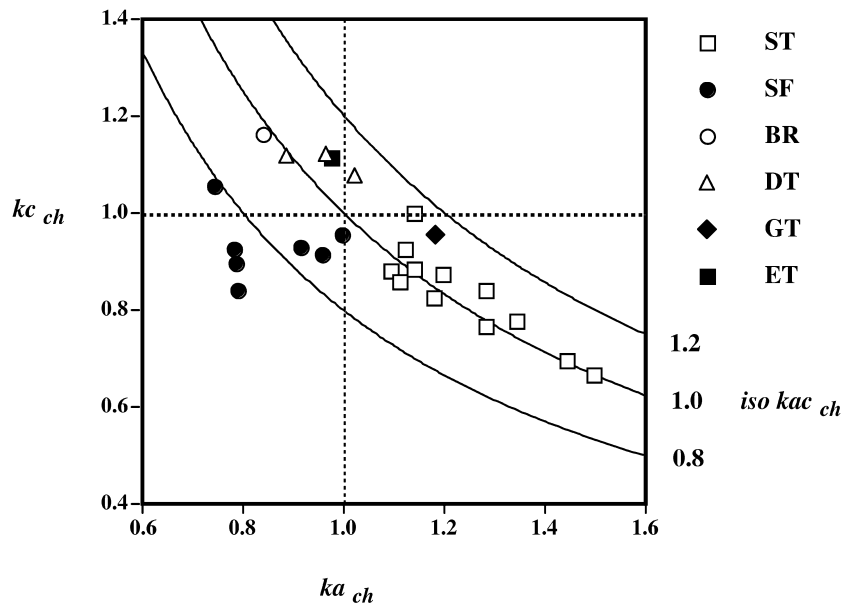
1. $k_{a, ch}$ was found to be greater than 1 whereas $k_{c, ch}$ was found to be less than 1; and
2. The greater the $k_{a, ch}$ the lower the $k_{c, ch}$.

The $k_{a, ch}$ and $k_{c, ch}$ values, as obtained from each of the studies investigated, are plotted against each other in Fig. 3, each point representing data as obtained from *homogeneous* groups of subjects (individual data for SF). In the figure, the (dotted) lines of no change in $k_{a, ch}$ and $k_{c, ch}$ (both equal to 1) divide the graph into four quadrants. In the top-left and bottom-right quadrants the increase of one variable is associated to the decrease of the other. In the top-right and bottom-left quadrants, the two variables increase or decrease simultaneously. In the figure, constant $k_{ac, ch}$ ($=k_{a, ch} \cdot k_{c, ch}$) values are represented by hyperbolas. Three such curves corresponding to $k_{ac, ch}$ equal to 0.8, 1.0 and 1.2 are shown. The points characterized by a measured change in power predicted by the measured change in CSA (Minetti 2002) must be located along the hyperbola for $k_{ac, ch} = 1.0$. The deviation from this curve is associated with a mismatch between the measured changes in power and in CSA. Along this hyperbola, a change of $k_{a, ch}$ is necessarily associated with a reciprocal change of $k_{c, ch}$. Hyperbolas for which $k_{ac, ch} \neq 1$ cross three quadrants; in such cases the changes of $k_{a, ch}$ and $k_{c, ch}$ are not simple mirror images of one another.

The framework introduced in Fig. 3 provides a new scheme for interpreting the adaptation of the motor system to training/detraining and to use/disuse. According to Enoka (1994) the neuro-mechanical changes due to chronic adaptation follow three general principles:

1. The overload principle, which states that adaptive responses occur only above a certain threshold
2. The specificity principle, which states that the induced change is specific to the exercise stress. This is indicated in Fig. 3 by the opposite changes in $k_{a, ch}$ and $k_{c, ch}$ in ST, GT and ET.
3. The reversibility principle, which states that training induced adaptations are transient. This is well described by the DT data: after ST, $k_{a, ch}$ decreases while $k_{c, ch}$ is bound to improve.

Fig. 3 The ka_{ch} and kc_{ch} values as obtained from each of the studies investigated are plotted against each other: *ET* explosive training, *GT* general training, *ST* strength training, *DT* detraining after strength training, *BR* bed rest, *SF* space flight (individual data). The three hyperbolae correspond to kac_{ch} equal to 0.8, 1.0 and 1.2 ($kac_{ch} = ka_{ch} \cdot kc_{ch}$), where *ch* indicates the post to pre ratio of the appropriate quantities. See text for details



It is shown in Fig. 3 that, apart from SF (full circles), all data seem to be clustered along the central hyperbola ($k_{ac, ch} = 1.0$). So, whereas the BR data seem to follow the basic principles reported above (mimicking the process of disuse observed in DT) the data obtained after space flight seem to behave differently. Therefore the data referring to BR and SF deserve a specific discussion, not only for this reason but also because the determinants of the loss of muscular power were discussed inadequately and inadequately reviewed in the corresponding papers.

Disuse and deconditioning

The effects of space flight (SF) and bed rest (BR) on the maximal explosive power of the lower limbs have only recently been investigated (Antonutto et al. 1998, 1999; Ferretti et al. 2001). Antonutto and coworkers (1999) discussed the decrease of peak or mean explosive power after SF in relation to the decrease in muscle mass. This last was estimated from measurements of cross-sectional area (CSA) of the calf muscles obtained using nuclear magnetic resonance (data from Zange et al. 1997) and assuming that the observed decrease in CSA was an estimate of the decrease in CSA of all the active muscles of the lower limbs. The rationale for this comparison was that a decrease of CSA (CSA_{ch}) smaller than that observed for power output (\dot{W}_{ch}) would imply that other mechanisms (e.g. an impaired motor unit recruitment pattern) must be responsible for the *residual* decline of power. Since the ratio \dot{W}_{ch} / CSA_{ch} was found to be 0.74 and 0.54 after 1 and 6 months respectively of SF, these authors concluded that neuromuscular “de-adaptation” had a great influence on power production, being responsible for about 26% and 46% of the decline in ex-

plosive power after SF of 1 and 6 months duration, respectively.

Ferretti and coworkers (2001) pointed out that the ratio \dot{W}_{ch} / CSA_{ch} (and hence the extent of the hypothesized neuromuscular *de-adaptation*) could easily be overestimated because the decrease of CSA due to immobilisation or weightlessness may not be homogeneously distributed among the flexor or extensor muscles of the lower limbs. Indeed they found that, after 42 days of BR, total thigh CSA (CSA_{tot} , assessed by nuclear magnetic resonance, MRI) was decreased less ($CSA_{tot, ch} = 0.874$) than the CSA of the extensors muscles ($CSA_{ext, ch} = 0.829$). They thus concluded that, after BR, the deficit in neural activation that could be hypothesized on the basis of the \dot{W}_{ch} / CSA_{ch} ratio, is more accurately determined (and is much smaller) when estimated on the basis of the appropriate quantity (CSA_{ext} rather than CSA_{tot}).

Whereas it is certainly true that more accurate measurements are desirable for understanding the relative importance of neural and muscular factors in the process of disuse/deconditioning, neither study took into consideration a more fundamental source of error: i.e. that the \dot{W}_{ch} / CSA_{ch} ratio is an erroneous indicator of neuromuscular de-adaptation because, as shown by Minetti (2002), \dot{W}_{ch} and CSA_{ch} are not linearly related.

The predicted values of \dot{W}_{ch} (obtained from Eq. 1 by substituting CSA_{ch} to $F_{use, ch}$) represent the change of power output that can be attributed to changes of muscle mass only. As a rule of thumb the difference between the measured and predicted values of \dot{W}_{ch} gives a rough indication of the effect of neural factors on the expression of maximal power output (it roughly corresponds to the value of $k_{ac, ch}$), even if the correct way to quantify the extent of neuromuscular de-adaptation is to compute all three constants: $k_{a, ch}$, $k_{c, ch}$ and $k_{ac, ch}$ (as indicated by Minetti 2002). As shown in Fig. 2, $k_{ac, ch}$

was found to be greatly affected by SF indicating that neural factors play indeed an important role in determining the decrease of power output. The individual values of $k_{ac, ch}$ after SF ranged from 0.948 to 0.652 depending on the duration of the flight, the extent of the counter-measures and the individual responses to the microgravity environment, whereas BR was found to affect $k_{ac, ch}$ to a lesser extent ($k_{ac, ch} = 0.959$). Even if the latter finding could be partially attributed to the shorter duration of the BR study (in respect to the average duration of SF), the observed differences between BR and SF in $k_{ac, ch}$ indicate that motor control and muscle co-ordination are affected to a greater extent in those situations in which the muscles have to adapt to the absence of gravity. This seems to be confirmed by the fact that $k_{a, ch}$ was similar after BR and SF (see Fig. 2) and hence that the similarity between the two conditions is confined to the *neuro-muscular level*. Indeed whereas $k_{c, ch}$ is less than 1 after SF, $k_{c, ch}$ is greater than 1 after BR (as found also for DT). This unexpected finding suggests that neuromuscular *impairment* in disuse, such as bed rest, has more analogies with the process of de-training than with the process of de-conditioning brought about by weightlessness. Finally, as shown by Fig. 3, BR data seems to follow the general relationship relating $k_{a, ch}$ to $k_{c, ch}$ in training and detraining whereas SF data seem to escape these boundaries. Indeed SF is the only condition for which all constants were found to be less than 1 (except for one subject where $k_{c, ch}$ is 1.045). Interestingly, this is the astronaut who spent less time in space (21 days).

Conclusions

As indicated by Minetti (2002), the chain of events leading from CSA changes to changes in power output can be split into two main conceptual steps. The first one leads from CSA (CSA_{ch}) to isometric force ($F_{iso, ch}$), the second one from $F_{iso, ch}$ to power changes (\dot{W}_{ch}). If these three quantities are measured before and after any experimental manipulation leading to muscle adaptation, the model proposed by Minetti allows the calculation of the post to pre ratios ($k_{a, ch}$ and $k_{c, ch}$) of two constants:

1. $k_a (= F_{iso}/CSA)$, expressing the contribution of *neuro-muscular/local factors* (e.g. muscle mass and architecture, recruitment pattern, fibre type, co-contractions, etc.); and
2. $k_c (= \dot{W}/F_{iso})$, expressing the contribution of *neural/central factors* (e.g. co-ordination of multiple joints and muscle groups, specificity of motor task, etc.). Therefore, the determination of these ratios allows one to investigate the role played by muscular – local factors ($k_{a, ch}$) – and/or by neural – central factors ($k_{c, ch}$) – in the adaptation process. In this paper these calculations have been applied to data reported in the literature concerning disuse, de-conditioning and de-training as well to data obtained after strength, explosive and general training. In spite of the non-

homogeneity of the data, and the coarse definition of *local* and *central* influences on the variables investigated, the picture emerging from these calculations confirms and extends the observations reported in the literature about the determinants of the adaptation process. In addition, the data reported and discussed above support the view that neuromuscular *impairment* due to disuse, as observed after bed rest, is closer to de-training than to the de-conditioning brought about by weightlessness. In this latter case in fact, the changes of the neural/central factors play an overwhelming role, which is not the case after bed rest. It is concluded that the quantitative approach presented in this paper offers a useful tool for analysing critically the factors involved in the training/detraining process.

Appendix

The maximal isometric strength of the knee extensor muscles (F_{iso}) was not measured in all the studies considered here. In the studies in which the peak dynamic force (F_p) was the only index of force reported (ST and GT), we calculated $F_{iso, ch}$ by assuming that peak dynamic force was about half of that developed isometrically ($F_{iso, ch} = 2 F_{p, ch}$). This last assumption was based on the following rationale.

On four astronauts/cosmonauts participating in the Euromir 94 mission (Antonutto et al. 1999), it was observed that the maximal force (F_p) that can be attained during an explosive jump on a sledge apparatus, is about half of that expressed during a maximal isometric contraction (unpublished observations). In these experiments two subjects (who remained in space for 31 and 169 days, see also Table 2) and their back ups were asked to perform maximal isometric contractions at the same knee and sledge angle utilized for assessing the maximal explosive power. In Table 3 the values of F_p and F_{iso} , as measured in the two pre-flight sessions for these four subjects, are reported. The ratio F_{iso}/F_p is

Table 3 The value of maximal force (F_p) that can be attained during an explosive jump on a sledge apparatus is about half of that expressed during a maximal isometric contraction (F_{iso}). In the first column M is the mass of the subject + the mass of the sledge (see text for details)

M g (N)	F_{iso} (N)	F_p (N)	F_{iso}/F_p	$n = F_{iso}/M$ g
1,040	3,196	1,537	2.08	3.1
1,059	2,892	1,781	1.62	2.7
1,167	3,117	1,697	1.84	2.7
1,118	2,522	1,117	2.26	2.3
1,040	3,206	2,271	1.95	3.1
1,059	2,333	1,728	1.91	2.2
1,167	3,627	1,840	2.01	3.1
1,118	3,440	1,887	2.04	3.1
			mean 1.96	mean 2.8
			(SD 0.19)	(SD 0.4)

equal to 1.96 (SD 0.19) and the calculated values of n ($n = 2F_p/Mg = 2.8$) are close to the value of 2.5 suggested by Minetti (2002). Since the calculations reported in Table 3 refer to experiments performed on a sledge apparatus, in this specific case, the mass of the subject was augmented by the mass of the sledge ($M = m + 41.4$ kg, see Antonutto et al. 1999).

In order to check that F_{iso} was estimated correctly, we compared our data with those reported by Zange and coworkers (1997) on four of the seven astronauts/cosmonauts considered in this paper. These authors measured, in addition to CSA (see text for details) also the maximal isometric force of the plantar flexors and found that F_{iso} decreased by about 20%–48% after the flight, corresponding to a $F_{iso,ch}$ of 0.755, on the average. This value is close to that calculated, on the same subjects, from $2 F_{p,ch}$ (0.733), thus supporting the assumption made in this paper in estimating $F_{iso,ch}$. The estimated values of $F_{iso,ch}$, $k_{a,ch}$ and $k_{c,ch}$ are indicated with an a in Tables 1 and 2 to be distinguished from the corresponding values as directly measured in all other conditions.

In order to solve Eq. 1 and 6, n should be known ($n = F_{iso}/mg$, e.g. the ratio between the body weight and the maximal isometric strength of the knee extensors). Even if it would have been better to calculate “individual” values of n instead of assuming a constant value (e.g. 2.5, as proposed by Minetti 2002) this was not possible in all cases (e.g. in all papers in which T_{max} instead of F_{iso} was reported, since the lever arm was not known). In those cases in which F_{iso} was directly measured, n was calculated and found to be 3.1 (SD 0.7); the data ranged from 1.7 (Häkkinen et al. 1998, 67 years-old females) to 4.3 (Ferretti et al. 2001, 28 years-old males). However, even when n is increased by a factor of 3, this leads to a difference of less than 1.5% in the prediction of \dot{W}_{ch} (see Eq. 1). Hence, assuming a constant value of 2.5, should not have affected the results to any significant extent.

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