



Invited review

Basic Science and Clinical Use of Eccentric Contractions: History and Uncertainties

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Abstract

The peculiar attributes of muscles that are stretched when active have been noted for nearly a century. Understandably, the focus of muscle physiology has been primarily on shortening and isometric contractions, as eloquently revealed by A.V. Hill and subsequently by his students. When the sliding filament theory was introduced by A.F. Huxley and H.E. Huxley, it was a relatively simple task to link Hill's mechanical observations to the actions of the cross bridges during these shortening and isometric contractions. In contrast, lengthening or eccentric contractions have remained somewhat enigmatic. Dismissed as necessarily causing muscle damage, eccentric contractions have been much more difficult to fit into the cross-bridge theory. The relatively recent discovery of the giant elastic sarcomeric filament titin has thrust a previously missing element into any discussion of muscle function, in particular during active stretch. Indeed, the unexpected contribution of giant elastic proteins to muscle contractile function is highlighted by recent discoveries that twitchin-actin interactions are responsible for the "catch" property of invertebrate muscle. In this review, we examine several current theories that have been proposed to account for the properties of muscle during eccentric contraction. We ask how well each of these explains existing data and how an elastic filament can be incorporated into the sliding filament model. Finally, we review the increasing body of evidence for the benefits of including eccentric contractions into a program of muscle rehabilitation and strengthening.

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A BRIEF HISTORY OF LENGTHENING MUSCLE CONTRACTIONS

As animals move through their environments, muscles must perform many functions to stabilize, propel, and decelerate their bodies. Muscles function not only as the source of work necessary for propulsion, but they are equally important in their function as brakes, converting kinetic energy of motion by recovering potential energy, or dissipating it as heat. For example, when moving downhill, gravity alone can result in sufficient kinetic energy that muscles must function as regulated brakes to decelerate the animal. Likewise, during running, because footfall always occurs before the center of mass moves over the foot, the first one-half of the stride necessarily

stretches the hip and knee extensors. If the energy absorbed during this phase of the stride is recovered during the muscle shortening cycle, then work done by the muscle is enhanced.

Lengthening (eccentric) muscle contractions are distinguished by several unique properties. In 1924, Fenn¹ may have been the first to observe that force production requires much less energy if a muscle is stretched while active (and more energy if shortening, the so-called *Fenn effect*). Decades later, his mentor A.V. Hill remained sufficiently puzzled by this observation to speculate that stretched muscle may function as an adenosine triphosphate generator (see Lindstedt² for a discussion). Perhaps the difference in energy requirement between lengthening and shortening contractions was best demonstrated by Abbott et al.³ using mechanically linked back-to-back stationary bikes. They showed that far less energy is required to resist than to propel the pedal movement.⁴ Additionally, and linked to increased energy efficiency,

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119 maximum muscle force is much greater during eccentric con- 176
120 traction than during shortening contraction.³ 177

121 MECHANISMS OF ECCENTRIC CONTRACTION 178

122
123 When active muscle is stretched, absorbing mechanical 179
124 energy, there are 2 fates of that energy: it can be lost as heat or 180
125 stored as elastic potential energy. This stored energy can 181
126 increase the work done during subsequent muscle shortening 182
127 while minimizing the energy cost. The stored energy is only 183
128 available for a short time, which likely sets stride frequency 184
129 during locomotion.⁵ There has been considerable speculation 185
130 as to how and where this energy is stored.^{6–10} However, ten- 186
131 dons outside the muscle and collagen within account for only 187
132 a small fraction (~4%) of energy storage.^{8,9} Thus the sarco- 188
133 mere itself must store most of the recoverable energy. There 189
134 are apparently only 2 candidates within the sarcomere that 190
135 could assume this function, the cross bridges and the giant 191
136 elastic titin filaments.¹¹ 192

137 Given that nearly a century has passed since the high-force 193
138 and low-energy cost of eccentric muscle contractions were first 194
139 described by Fenn,¹ it is surprising that so little progress has 195
140 been made in identifying the biophysical and biochemical 196
141 basis for these muscle properties that play important roles in 197
142 the biomechanics and control of movement.¹² Herein, we 198
143 review the alternative hypotheses, attempt to understand why 199
144 definitive answers have not been forthcoming, and suggest 200
145 potentially fruitful experiments that could help to rule out 201
146 alternative hypotheses. The history of the discovery of mech- 202
147 anisms underlying the “catch” phenomenon in muscles of inver- 203
148 tebrates, which shares many features with eccentric 204
149 contraction in vertebrate muscles, suggests some potential 205
150 approaches. 206

151 FORCE ENHANCEMENT DURING STRETCH OF 207

152 ACTIVE MUSCLE 208

153 Because the only active players in muscle sarcomeres were 209
154 long thought to be actin–myosin cross bridges, until recently 210
155 nearly all mechanistic theories of eccentric contraction attrib- 211
156 uted the increased force during and after stretch of active 212
157 muscles to cross-bridge properties.^{6,7,13,14} Reverse engineer- 213
158 ing—deducing the function of the cross bridges from the mac- 214
159 roscopic behavior of muscles—is a valuable scientific tool for 215
160 generating new hypotheses. Deductive reasoning, however, is 216
161 less useful for hypothesis testing because it is prone to hidden 217
162 and usually untested assumptions and can lead down a spuri- 218
163 ous path (eg, Hill’s adenosine triphosphate generation) when 219
164 assumptions are false or important facts are missing. Although 220
165 the goal of muscle physiology should instead be to predict the 221
166 macroscopic behavior of muscle from an understanding of the 222
167 properties of its component parts,¹⁵ the practicality of a more 223
168 inductive approach is limited by the technical challenges of 224
169 measuring cross-bridge properties directly. Yet if we are nec- 225
170 essarily constrained to using a deductive approach, it is all the 226
171 more important to acknowledge its limitations. 227

172 Force enhancement in muscles during and after active 228
173 stretching is a classic example of deductive reasoning. The 229
174 230
175 231

176 standard and nearly universal approach has been to measure 177
178 the macroscopic properties of stretched muscle and infer the 179
180 properties of the cross bridges directly from these measure- 180
181 ments,^{6,7} explicitly or implicitly assuming that the cross 181
182 bridges alone are responsible for producing the macroscopic 182
183 properties. Despite the evident circularity of this reasoning, it 183
184 has become surprisingly difficult even to suggest that there is 184
185 room for alternative mechanisms. 185

186 Although there is no fundamental theoretical problem with 186
187 cross bridges storing energy during stretch, their small size, 187
188 short duration of attachment, and rapid detachment from 188
189 actin¹⁵ impose significant constraints on their ability to store 189
190 energy. To explain the lower energy cost of eccentric contrac- 190
191 tions, cross-bridge models require ad hoc assumptions. Untest- 191
192 able assumptions regarding cross-bridge properties, such as 192
193 stiffness, duty ratio, and energy states, are therefore required 193
194 for estimating the potential of cross bridges to store energy 194
195 during stretch. Early work assumed that all of the instantane- 195
196 ous elasticity of muscle resides in the cross bridges¹³ and 196
197 that the cross bridges alone account for all of the increased 197
198 force during stretch.^{6,7} Yet, by 2003, the estimated contribu- 198
199 tion of cross bridges to energy storage during active muscle 199
200 stretch was only 12%, with cross-bridge elasticity accounting 200
201 for a mere 2% of the energy.⁹ To understand this change in the 201
202 perceived contribution of cross bridges to active stretch, it is 202
203 instructive to examine this history in greater detail. 203

204 Assuming that “there is a virtually instantaneous elasticity 204
205 within each cross bridge,” Huxley and Simmons¹³ concluded 205
206 “we now believe that the instantaneous elasticity (or at least 206
207 the greater part of it) resides in the cross bridges themselves.” 207
208 Lombardi and Piazzesi⁶ made careful measurements showing 208
209 that the force during active lengthening of isolated frog muscle 209
210 fibers was nearly double the isometric force. On the basis of 210
211 these experiments, they concluded that “steady lengthening of 211
212 muscle fibers induces a cross-bridge cycle characterized by 212
213 fast detachment of cross bridges extended beyond a critical 213
214 level.” Their mathematical model suggested that 214
215 “reattachment of forcibly attached cross bridges is 200 times 215
216 faster than attachment of cross bridges which detach after 216
217 completion of the cycle.” This deductive model was developed 217
218 further by Piazzesi and Lombardi.⁷ 218

219 Two different lines of evidence contributed to the changing 219
220 view of cross bridges between 1995 and 2003. The first was 220
221 the observation from molecular motors that the duty ratio of 221
222 myosin II in muscle sarcomeres must necessarily be low, 222
223 likely <20% and possibly much lower, because the distance 223
224 between successive binding sites on actin (~36 nm) is too far 224
225 to be traversed within a single cross-bridge cycle.¹⁶ The con- 225
226 clusion, now generally accepted,¹⁷ is that the number of cross 226
227 bridges attached at any given time (~20%) is only a small 227
228 fraction of the value (77%) typically assumed in previous stud- 228
229 ies^{6,7} and rationalized on the basis of x-ray diffraction and 229
230 other empirical observations. The debate is nicely captured in 230
231 Huxley’s letter to the editors and Howard’s reply.¹⁸ 231

232 The second line of evidence was the observation that the 232
233 compliance of the thin¹⁹ and thick filaments²⁰ also contributes 233
234 significantly (~70%) to muscle compliance, so that muscle 234

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