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Swimming training increases the G_4 acetylcholinesterase content of both fast ankle extensors and flexors

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The effect of endurance swimming training on AChE molecular forms was examined in 2 groups of functionally antagonist rat muscles, including ankle extensors and flexors. This exercise regimen, which entails predominant dynamic activity (i.e., involving extensive shortening) of both groups of muscles, resulted in marked selective G_4 increases in all fast muscles. The G_4 elevation exhibited by the ankle flexors was in sharp contrast to the G_4 reduction reported in these same muscles following running training, during which their action is predominantly tonic. The results strengthen the conclusion that predominantly dynamic activity increases the G_4 content of mature innervated fast muscles.

Acetylcholinesterase molecular form; Acetylcholinesterase adaptation to activity; Muscle plasticity; Exercise

1. INTRODUCTION

Innervated mature fast muscles of rodents characteristically differ from their slow-twitch counterparts by exhibiting high levels of G_4, the tetrameric form of AChE (see refs in [1]). Converging lines of evidence suggest that this peculiar G_4 pool bears a special functional significance, distinct from that of the junction-associated asymmetric forms (see refs in [1]). In particular, G_4 is subject to a selective regulation, independent from that controlling the asymmetric forms [1,2]. Moreover, in contrast to the asymmetric forms, the G_4 pool specific to fast muscles is highly sensitive to the functional demands placed upon the muscle [1,2]. On the basis of the ensemble of the available data, it has been proposed that, in innervated mature fast muscles, the G_4 content depends more on the type of activity the muscle actually performs than on the type of its motor innervation [3]. This hypothesis has recently received strong support from a study showing that endurance running training selectively induces marked opposite G_4 changes in functionally antagonist fast muscles [1]. Whereas G_4 increased by more than 50% in the fast ankle extensors gastrocnemius (GAST) and plantaris (PL), which play a dynamic role (i.e., involving extensive shortening) in this particular exercise, the amount of tetramer was reduced by about 40% in the fast ankle flexors tibialis anterior (TA) and extensor digitorum longus (EDL) which, during running, exhibit a predominant tonic activity (i.e., involving a significant isometric component). These results support the view that, in innervated mature muscles, the size of the G_4 pool depends on the predominant type, dynamic or tonic, of activity actually performed.

In an attempt to strengthen this conclusion, we subjected rats to an alternative exercise model consisting of an endurance swimming training program. We chose this type of exercise because, in opposition to running, swimming entails a clear dynamic activity of both ankle extensors and flexors [4]. We therefore anticipated the swimming training program to result in a G_4 increase in the 2 groups of muscles, including the fast ankle flexors TA and EDL.

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2. MATERIALS AND METHODS

2.1 *Training program*

Female Sprague–Dawley rats (180–200 g) were housed individually in steel wire cages kept in a temperature-controlled room at 20°C and maintained on a 12 h/12 h light–dark cycle. They were provided with water and food (Purina rat chow) ad libitum. One week following arrival to our animal facilities, a group of rats was randomly selected to undergo an endurance swimming training program. The swimming regimen consisted of swimming twice a day, for 12–15 weeks, in a tub filled with water kept at 33°C. In order to ensure effective swimming by the rats, the water was continuously agitated by bubbling with compressed air. The initial 10-min swimming time was gradually increased until the animals swam 90 min, twice a day, by the third week. The training rats were returned to their cages between the exercise sessions. Control rats were cage-confined.

2.2 *Tissue preparation*

Twenty four hours following the last swimming session, the muscles to be analyzed were removed from the trained as well as control rats anesthetized with Na-pentobarbital (35 mg/kg, i.p.), immediately frozen in melting isopentane precooled with liquid N_2 and subsequently kept at −80°C. Whole frozen muscles were later homogenized in a high salt, detergent buffer containing anti-proteolytic agents [1].

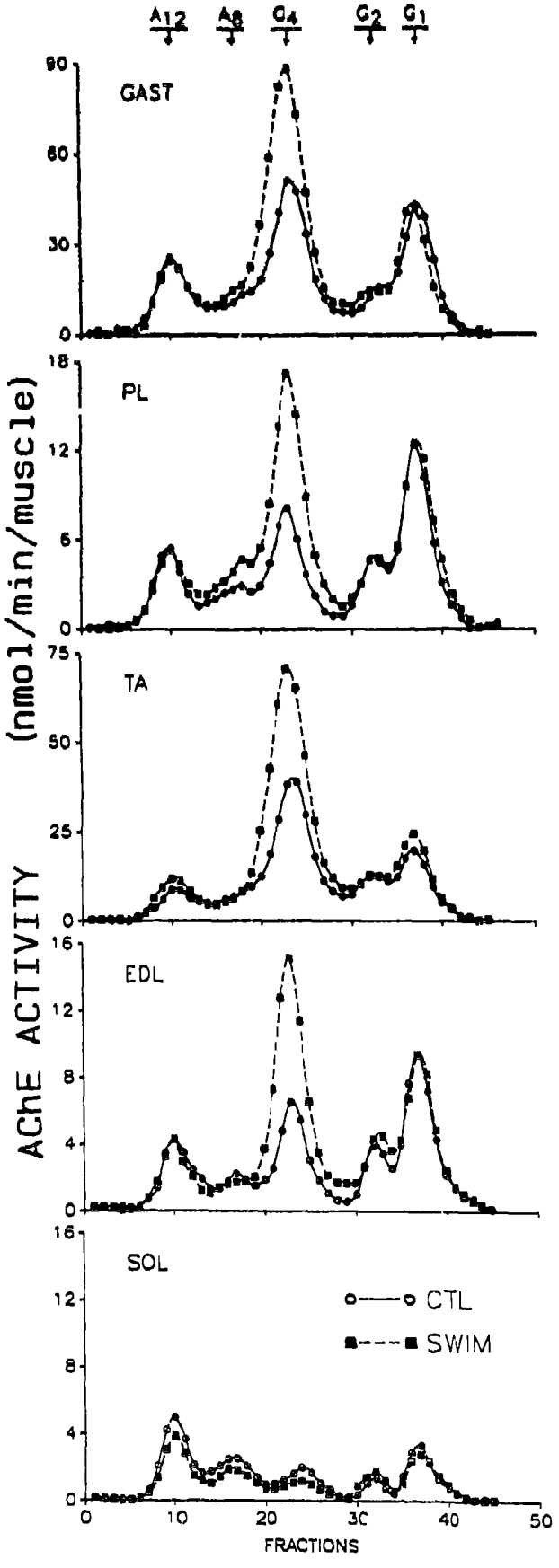

Fig. 1. Effect of swimming training on AChE molecular forms of functionally antagonist muscles of the rat hindlimb. Shown are actual distributions that are representative of the average content in AChE molecular forms observed in 10–14 specimens of each control and trained muscle. The distribution of molecular forms is expressed as activity per muscle as computed from the overall activity per muscle and the sedimentation profile. The AChE distribution of SOL is represented on the same scale as that of EDL, which exhibits similar amounts of A_{12}.

2.3. *Biochemical analysis*

Citrate synthase (EC 4.1.3.7) activity was assayed according to Srere [5]. AChE measurements, sedimentation analyses of the AChE molecular forms as well as processing of the raw data were performed as described in detail elsewhere [1,3]. The effect of training on the individual AChE molecular forms was evaluated by comparing their average activity per muscle, in control and trained muscles (n = 10–14). Comparison of the specific activities yielded similar results (not shown). Statistical analysis was performed between group means using 2-tailed Student's t-test with a level of significance selected at the 0.05 level.

3. RESULTS

3.1. *General effects of swimming training*

Following the training program, the mean body weight of the trained rats was very similar to that of controls (about 290 g). The trained muscles showed no obvious signs of hypertrophy, and the protein concentration in the extracts of trained muscles was unchanged (100–109%) as compared to the controls. The activity of the mitochondrial enzyme citrate synthase was increased slightly although significantly in all 5 trained muscles examined (13–18%; $P < 0.05$). Such a relatively modest adaptation of the muscle's oxidative capacity to swimming training, as compared to that induced by running training (35–38%) [1], is in agreement with what has been reported [6].

3.2. *Effect of swimming training on AChE*

The most distinctive effect of training was seen on G_4 whose content increased markedly in all 4 fast muscles (Fig. 1). In the fast ankle extensors GAST and PL, the level of tetramer was selectively augmented by 67% and 105% ($P < 0.0005$), respectively, with no significant change in the level of any other molecular form. In the fast ankle flexors TA and EDL, G_4 was elevated by 52% and 126% ($P < 0.005$), respectively. However, the flexors exhibited slight increases in the contents of other forms as well: in TA, A_{12} and G_2 were augmented by 21% and 26% ($P < 0.05$), respectively, whereas, in EDL, G_2 was increased by 42% ($P < 0.01$).

By contrast, in the case of the slow-twitch extensor SOL, swimming training induced a small decrease in AChE content: A_8 and G_4 were reduced to 83% and 75%, respectively ($P < 0.05$). It is noteworthy that although these reductions were significant, they involved only low amounts of AChE activity.

4. DISCUSSION

The present results strongly confirm that, as shown by 2 previous studies [1,2], elevation of the level of natural activity selectively affects the pool of G_4 characterizing fast muscles, while altering only marginally, if at all, the other AChE molecular forms, in particular the asymmetric forms.

However, the most significant finding provided by this study is the observation that swimming training induced a marked G_4 increase in the ankle flexors TA and EDL, in sharp opposition to the pronounced tetramer reduction displayed by these same muscles following running training [1]. Actually, the divergence of the G_4 changes exhibited by the fast ankle flexors following running and swimming training reflects the disparity in the type of biomechanical action performed by these muscles during the 2 exercises. Indeed, during running, TA and EDL contract for most of the time against the inertial torque generated at the ankle by protraction of the hindlimb, counteracting stretching forces [1,7]. By contrast, during swimming, the ankle flexors contract against water resistance with extensive shortening, as do the extensors, and thus both groups of muscles exhibit a clear dynamic activity [4]. The G_4 increase displayed by the ankle flexors following swimming training significantly strengthens the proposal that the G_4 content of the fast muscles is high or low according to whether the actual activity the muscle is called upon to perform is predominantly dynamic or tonic [1].

In opposition to the fast muscles, the slow-twitch SOL responded to swimming training by minor and non-specific AChE changes which, interestingly, were very similar to the AChE alterations induced by running [1]. This is striking considering that, in contrast to its action during running, SOL plays no anti-gravity role during swimming, although it is significantly activated as attested by its increased citrate synthase activity, and EMG [8]. This peculiar insensitivity of SOL AChE to exercise might be related to the fact that SOL already performs its anti-gravity function in cage-confined animals for extended periods of time. Hennig and Lomo have shown that, in sedentary rats, SOL is active for at least 5 h per day, whereas, by contrast, the total active time of EDL per 24 h does not exceed 72 min [9,10]. These marked differences in amount of daily activation might explain why superimposed running [1] and swimming sessions lasting 2 and 3 h per day, respectively, are able to modify the G_4 level of EDL, but have only a minor impact on the AChE content of SOL. Altogether, these facts are consistent with the possibility that the G_4 content of a mature innervated muscle is determined by the type of activity the muscle is performing for the longest duration.

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