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RESEARCH NOTE

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Motor unit properties after operant conditioning of rat H-reflex

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Abstract Operant conditioning of the H-reflex produces plasticity at several sites in the spinal cord, including the motoneuron. This study assessed whether this spinal cord plasticity is accompanied by changes in motor unit contractile properties. Thirty-one adult male Sprague-Dawley rats implanted for chronic recording of triceps surae electromyographic activity and H-reflex elicitation were exposed for at least 40 days to HRup or HRdown training, in which reward occurred when the H-reflex was greater than (12 HRup rats) or less than (12 HRdown rats) a criterion value, or continued under the control mode in which the H-reflex was simply measured (7 HRcon rats). At the end of H-reflex data collection, rats were anesthetized and the contractile properties of 797 single triceps surae motor units activated by intra-axonal (or intramyelin) current injection were determined. Motor units were classified as S, FR, Fint, or FF on the basis of sag and fatigue properties. Maximum tetanic force and twitch contraction time were also measured. HRdown rats exhibited a significant increase in the fatigue index of fast-twitch motor units. This resulted in a significant decrease in the percentage of Fint motor units and a significant increase in that of FR motor units. HRup conditioning had no effect on fatigue index. Neither HRup nor HRdown conditioning affected maximum tetanic force or twitch contraction time. These data are consistent with the hypothesis that conditioning mode-specific change in motoneuron firing patterns causes activity-dependent change in muscle properties.

Keywords Plasticity · H-reflex · Operant conditioning · Triceps surae · Motor unit type

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Introduction

The spinal reflex pathway that mediates the first response to limb displacement (i.e., the spinal stretch reflex), or to electrical stimulation of large-diameter sensory afferents (i.e., the H-reflex), can be operantly conditioned (see Wolpaw and Tennissen 2001 for review). Rats, monkeys, and humans can gradually increase or decrease the size of these reflexes to increase the probability of reward (Wolpaw et al. 1983; Wolpaw 1987; Evatt et al. 1989; Chen and Wolpaw 1995; Wolf and Segal 1996). This conditioning is associated with plasticity at multiple sites in the spinal cord (Wolpaw and Lee 1989; Wolpaw et al. 1989; Feng-Chen and Wolpaw 1996). Thus it is likely to modify motoneuron firing behavior. For example, the change in motoneuron firing threshold associated with conditioned decrease in the H-reflex (Carp and Wolpaw 1994) is likely to alter motoneuron responses to numerous central and peripheral inputs. The changes in motoneuron synaptic terminals accompanying H-reflex conditioning, and the probable interneuronal changes, are also likely to affect motoneuron activity (Carp and Wolpaw 1995; Feng-Chen and Wolpaw 1996).

Long-term modifications in motoneuron activity can affect motor unit properties (Gordon and Pattullo 1993; Pette 1998). Thus, the probability that H-reflex conditioning changes motoneuron firing behavior also raises the possibility that it also produces activity-dependent changes in motor unit properties. Type-specific changes might modify motor unit recruitment and thereby affect the number and/or firing rates of the motor units that comprise the fixed level of background electromyographic activity (EMG) that precedes H-reflex elicitation and/or might affect the recruitment of motor units into the H-reflex (Jones and Bawa 1999). Change in motor unit properties might also trigger additional plasticity necessary to maintain correct performance of other behaviors (Wolpaw and Tennissen 2001).

To learn whether H-reflex conditioning has effects on motor unit contractile properties that could contribute to H-reflex change, we studied single motor units from rats that had been rewarded for increasing (HRup rats) or decreasing the H-reflex (HRdown rats) and from control rats in which the H-reflex had simply been measured without imposition of any reward contingency (HRcon rats). Portions of the data from HRup and HRdown rats have been reported in abstract form (Carp et al. 1999a).

Materials and methods

Experiments were performed in 31 male Sprague-Dawley rats (308–475 g). All procedures adhered to the Guide for the Care and Use of Laboratory Animals of the Institute of Laboratory Animal Resources, Commission on Life Sciences, National Research Council (National Academy Press, Washington, DC, 1996) and had been reviewed and approved by the Institutional Animal Care and Use Committee of the Wadsworth Center. Methods for electrode implantation, H-reflex conditioning, and motor unit study have been described previously (Chen and Wolpaw 1995; Carp et al. 1999b, 2001a) and are summarized here, except where methodological differences require more detailed description.

H-reflex conditioning

Rats chronically implanted in the right leg with a nerve cuff on the posterior tibial nerve at the level of the knee and with EMG recording electrodes in triceps surae (TS) muscles (i.e., soleus, SOL), and medial and lateral gastrocnemii (MG and LG) received a nerve cuff stimulus whenever background EMG remained within a defined range for a randomly varying 2.3- to 2.7-s period (mean number of daily stimuli ± SD = 4289±1655). Data were collected for 10–28 days in HRcon mode (i.e., no reward contingency) to determine each rat's initial H-reflex size. Rats were then exposed to the HRup mode (*n*=12) or HRdown mode (*n*=12) for at least 40 days, during which they received a food pellet reward if the H-reflex was above (HRup) or below (HRdown) a criterion value, or they were continued in HRcon mode (*n*=7) for 71–225 days (except for one rat in which data collection was stopped after 24 days due to electrode failure). All rats remained healthy and active throughout the several months of data collection and had similar weight gains.

Animal preparation for motor unit study

At the end of H-reflex data collection, rats were anesthetized with pentobarbital (60 mg/kg i.p. initially, supplemented with 10 mg/kg i.v. about every 30 min to suppress corneal and limb withdrawal reflexes and maintain heart rate between 300 and 350 bpm) and secured in the prone position in a rigid frame by ear and jaw bars, hip pins, and pins through the right knee and ankle. The TS muscles of the right hindlimb were dissected from surrounding tissue and the calcaneus was cut, leaving the TS tendon attached to a small bone chip, which was connected to a force transducer. A pair of fine Teflon-insulated stainless steel wires were inserted into each of the TS muscles for recording EMG. A chamber surrounding the entire rear portion of the rat was filled with mineral oil and thermostatically controlled to maintain hindlimb temperature at 36–37 C.

In preparation for axon impalement in the ventral root, a dorsal laminectomy was performed from the L1 to the L5 vertebrae and the dura mater was cut. The cut skin flaps were retracted to hold a 37–38 C mineral oil pool, within which a L5 or L6 ventral root was mounted on a pair of stainless steel hook electrodes.

Single motor unit recording

Ventral root axons (or their myelin sheaths) were impaled with glass microelectrodes (3 M potassium acetate, 12–25 MΩ). TS motor units were identified by the presence of reproducible all-ornone EMG and twitch responses to single stimuli over at least a fourfold range of current intensities. While SOL alone was monitored during H-reflex conditioning in most rats, we studied motor units from all three TS muscles (i.e., SOL, MG, and LG) because primate data indicated that conditioning of SOL, MG, or LG has comparable effects on all three muscles (Carp and Wolpaw 1994, 1995) and because, in the smaller muscles of the rat especially, the chronic EMG electrodes implanted in SOL reflect activity in MG and LG as well.

The following sequence of stimulation and recording protocols was initiated and continued until it was completed or until the unit was lost. First, 4–16 individual twitches were recorded during 0.2 Hz stimulation and averaged. Second, tetanic force was recorded during five to ten stimulus trains (600 ms long at 200 Hz). Third, in order to detect sag, force during partially fused contractions was recorded during 4–8 trains of 25 stimuli (with interstimulus intervals in the range of 1–4 times the twitch contraction time) repeated at 10-s intervals (Carp et al. 1999b). Fourth, fatigue was assessed by recording force during application of 70-Hz trains of 14 stimuli delivered at 1-s intervals for 2 min. [Motoneuron axonal conduction velocity, also measured for most units, is reported elsewhere (Carp et al. 2001a).]

Recording stability limitations precluded an extensive search for the passive force producing maximal contractile force for each unit. Thus, we adjusted muscle length to maintain whole-muscle passive force within a narrow range (mean background passive force ± SD = 140±13 mN for all motor units; range = 99–183 mN).

TS whole muscle twitch in response to supramaximal stimulation of the tibial nerve was monitored every 2–4 h during the course of the recording session, which normally lasted 8–12 h. Recording was terminated when twitch force fell below 75% of its initial value. At the end of recording, the rat was sacrificed with an overdose of i.v. pentobarbital.

Analysis of motor unit data

Contraction time was calculated from the averaged twitches. Peak tetanic force was calculated for each of the tetani to determine the maximum tetanic amplitude. The presence or absence of sag was noted for all tetani tested in each motor unit. Motor units were classified according to the criteria of Burke et al. (1973) as modified by Carp et al. (1999b). Motor units that exhibited sag during at least one unfused tetanus were classified as fast-twitch (F); those units that did not exhibit sag in any of at least four unfused tetani at different interstimulus intervals were classified as slow-twitch (S). F motor units were further subdivided according to their fatigue index (i.e., the ratio of the maximum force during the 120th tetanus to that during the first tetanus). F motor units with a fatigue index ≥0.75 were classified as fatigue-resistant (FR), those with 0.25 < fatigue index < 0.75 as having intermediate fatigability (Fint), and those with fatigue index ≤0.25 as fatigue-sensitive (FF).

The percentage of each of the four types of motor units was calculated for each rat. Differences in the distribution of motor unit types among conditioning modes were assessed by one-way analysis of variance, with differences between HRcon and HRup or HRdown rats determined by Dunnett's test. Differences in contractile properties among conditioning modes were assessed by nested analysis of variance, with conditioning mode as the main factor, animals nested within conditioning mode, and measurements from individual motor units nested within animals. This statistical method assesses the conditioning groups with respect to between-subject differences independently of within-subject differences (i.e., differences in the numbers and variability of measurements performed in individual rats). Intergroup differences were assessed by multiple contrasts (JMP, SAS). For all statistical tests, differences for which *P* was less than 0.05 were considered to be statistically significant.

Statistical analysis was potentially complicated by two factors: rat age and implant duration. Distributions of rat motor unit contractile properties change with age (Kugelberg 1976; Ripoll et al. 1979; Edström and Larsson 1987). However, linear regression analysis failed to find any significant dependence of tetanic force, contraction time, and fatigue index on body weight or implant duration among all animals ($P>0.1$ for all regressions). Furthermore, inclusion of body weight and implant duration in the analysis described above did not alter the dependence of motor unit properties on conditioning mode. We attribute these findings to the minimal intergroup differences in weight and to the lack of long-term direct effects of the implanted EMG wires on muscle contractile properties (Carp et al. 2001b).

Results

Background EMG amplitude, M response size, and number of trials per day remained stable throughout data collection in HRup, HRdown, and HRcon rats. H-reflex conditioning was successful (i.e., ±20% change in the correct direction; Wolpaw et al. 1993; Chen and Wolpaw 1995) in 9 of the 12 HRup rats (75%) and 9 of the 12 HRdown rats (75%). In the nine successful HRup rats, mean H-reflex size ± SEM rose to 163±11% of its control mode value (range = 122–221%), and in the nine successful HRdown rats it fell to 49±7% (range = 18–78%). In each of the six unsuccessful rats and the seven HRcon rats, final H-reflex size was within 20% of its control-mode value (range = 83–117%). Successful HRup and HRdown rats are subsequently referred to as HRup+ and HRdown+ rats, respectively, while unsuccessful HRup and HRdown rats are referred to as HRup– and HRdown– rats, respectively.

We studied 797 TS single motor units in the 31 rats (median number per rat = 25, range = 11–38). Analysis focused on the 197 motor units from the 7 HRcon rats, the 256 from the 9 HRup+ rats, and the 197 from the 9 HRdown+ rats. The smaller populations from the 3 HRup– and the 3 HRdown– rats (61 and 86 motor units, respectively) provided some insight into whether successful conditioning or merely exposure to the conditioning protocol was associated with motor unit change.

HRdown conditioning altered fatigue sensitivity. The average fatigue index was significantly higher for the F motor units from HRdown+ rats than for those from HRcon rats (mean of average fatigue index from each rat ± SEM = 0.66±0.03 and 0.55±0.04 for HRdown+ and HRcon rats, respectively, $P<0.05$). No difference in fatigue index was observed between the S motor units of HRdown+ rats and those of HRcon rats (0.97±0.00 and 0.99±0.01, respectively). An effect on fatigue index similar to that in HRdown+ rats was evident in the three HRdown– rats (0.65±0.03 and 0.98±0.00 for F and S motor units, respectively). On the other hand, no effects on fatigue sensitivity with respect to HRcon rats were detected in HRup+ rats (0.60±0.02 and 0.96±0.01 for F and S motor units, respectively) or HRup– rats (0.62±0.09 and 0.94±0.05 for F and S motor units, respectively).

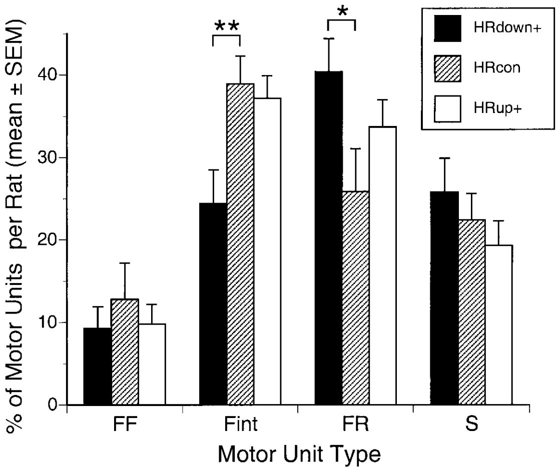

Fig. 1 Distribution of the four types of motor units from HRdown+, HRcon, and HRup+ rats. *Each bar* represents the mean percent of motor units (i.e., 100 × number of motor units of a given type/total number of typed motor units for each rat) ± SEM for all rats in the conditioning group. The average proportion of FR motor units increased and that of Fint motor units decreased significantly after successful HRdown conditioning (*$P<0.05$, **$P<0.005$)

The shift in fatigue sensitivity was also expressed as a change in the motor unit type distribution (Fig. 1). In HRcon rats, Fint was the most common motor unit type [39±3% (mean % of total number of typed motor units in each rat ± SEM)], and FR was the next most common (25±5%). This order was reversed in HRdown+ rats: FR was most common (40±4%) and Fint was next most common (24±4%). The Fint and FR differences were both significant: Fint units were less frequent and FR units more frequent in HRdown+ rats than in HRcon rats ($P<0.005$ and $P<0.05$, respectively). While HRcon and HRdown+ rats were not significantly different in frequency of FF or S motor units, the tendency in HRdown+ rats towards a decrease in FF motor units and an increase in S motor units was consistent, with an overall shift in motor unit type distribution toward the fatigue-resistant end of the normal spectrum. Similar results were obtained when contraction time was used to classify motor units as fast (contraction time <20 ms) or slow (contraction time ≥20 ms) instead of sag (i.e., average percentages of Fint motor units 37±3% and 26±4% and that of FR motor units 32±4% and 42±5% in HRcon and HRdown+ rats, respectively). Motor units from the three HRdown– rats showed a similar shift in distribution (i.e., 30±8% Fint and 41±9% FR). Thus, the distribution shift did not appear to depend on the magnitude of the conditioning-induced decrease in the H-reflex. No significant or consistent changes were found in the type distribution of motor units from HRup+ rats (Fig. 1) or from the three HRup– rats.

No statistically significant type-specific differences were observed in tetanic force and contraction time between HRcon and HRdown+ or HRup+ rats. Furthermore, HRdown+ and HRup+ rats did not differ from HRcon rats in average values of tetanic force and contraction time for F motor units alone or for all F and S motor units together.

Discussion

The present results show that HRdown conditioning increased fatigue resistance without disrupting the normal relationships among fatigue sensitivity, force generation, and contraction time. This change does not appear to result from differences in factors unrelated to conditioning. While motor unit contractile properties can differ with animal age (Luff 1998), the close similarity among HRdown, HRup, and HRcon rats in weight, the absence of detectable weight effects on the data, and previous evidence that properties change little over the weight (and presumably age) range used in the present study (Ripoll et al. 1979; Alnaqeeb and Goldspink 1987) indicate that age cannot account for the observed effect of HRdown conditioning on fatigue sensitivity. Furthermore, while reinnervation can alter motor unit properties (Gordon and Pattullo 1993), the modest degree of denervation associated with the chronically implanted nerve cuff is not sufficient to change motor unit type distribution (Carp et al. 2001b) and – most important – HRdown, HRup, and HRcon rats were all similarly implanted. Thus, the difference in fatigue sensitivity is not attributable to reinnervation-induced changes in motor unit type.

Given the absence of age or injury effects, the differences in motor unit type distribution are most likely to reflect activity-dependent plasticity in motor unit properties caused by the H-reflex conditioning protocol. Motor unit contractile and histochemical properties are sensitive to the pattern, frequency, and total amount of their activity (Gordon and Pattullo 1993; Pette 1998). Chronic low-frequency stimulation of a muscle nerve induces a transformation of motor units from F to S (Gordon et al. 1997). In addition to frequency of activation, the absolute amount of activity experienced by motor units contributes to respecification of motor unit type (Kernell et al. 1987a, 1987b). Chronic endurance training is associated with physiological alterations in contractile properties, including increased fatigue resistance (Barnard et al. 1970; Fitts et al. 1973; Fitts and Holloszy 1977), and shifts in expression of myosin heavy chain (MHC) isoforms from IIb to IIx to IIa (Sugiura et al. 1990; Haddad et al. 1998). In the present study, the finding that HRdown conditioning was associated with a shift to greater fatigue resistance among F motor units is consistent with the hypothesis that this conditioning mode affects motoneuron firing patterns, which in turn results in activity-dependent change in motor unit properties. The lack of detectable effect on S motor units in the present study may reflect insufficient time for or innate limitations on such a transformation (Kirschbaum et al. 1990; Leeuw and Pette 1993; Putman et al. 1999).

Activity-dependent changes in motor unit contractile properties in HRdown rats cannot be attributed to repeated application of the H-reflex stimulus because the number of stimuli did not differ among HRcon, HRup, and HRdown rats. Furthermore, the orthodromic activation of large motor axons by the low intensity stimulus would be expected to produce a greater effect on the contractile properties of FF units than on those of Fint and FR units, in which the greatest changes were actually observed. Thus, it is likely that the HRdown conditioning mode induces a chronic change in motor unit activity. HRdown rats spent 8–16% of each day providing the background EMG required prior to H-reflex elicitation. This represents a longer daily exposure to an altered activation pattern than the 5% daily exposure to chronic electrical stimulation that elicited an increase in fatigue resistance (Kernell et al. 1987a). Thus, if the HRdown mode induces a change in the number, identity, or firing rate of the subset of motor units that provides this background activity, it might account for the change in motor unit fatigue properties (Fig. 1).

The lack of symmetry between the effects of HRup and HRdown conditioning on motor unit properties and on the spinal cord (Carp and Wolpaw 1994, 1995; Carp et al. 2001a) suggests that HRup and HRdown rats use different strategies to increase the probability of reward in the operant paradigm. Because the change in fatigue sensitivity appears to occur in both successful and unsuccessful HRdown rats, the conditioning-induced effects on motor unit contractile properties may depend more on the strategy that the conditioning mode induces than on the behavioral outcome of its employment. In addition, these effects on contractile properties cannot be attributed to changes in motoneuron discharge behavior resulting from HRdown conditioning-induced effect on motoneuron firing threshold, because the threshold effect occurs only with successful HRdown conditioning (Carp and Wolpaw 1994).

Theoretically, HRdown-induced changes in motor unit discharge behavior could indirectly contribute to the observed changes in H-reflex size. Chronic change in motor unit activity by electrical stimulation can alter both motoneuron and muscle properties (Gordon et al. 1997; Munson et al. 1997). The extent to which altered motor unit properties contributes to H-reflex change is difficult to estimate directly from the present data, because they do not necessarily reflect the properties of the subset of motor units that contributes to the H-reflex in the behaving rat. Determination of whether motor unit properties actually contribute to conditioned H-reflex change requires assessment of motor unit activity in the behaving rat over the course of conditioning (Carp et al. 2000; Schalk et al. 2000).

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