PERSPECTIVES

The continuing debate about CNS control of proprioception

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More axons are devoted to transmitting signals to and from muscle spindles than to activating the muscles themselves. This implies not only an important role for the sensory signals from muscle spindles, but also the need to adjust these signals at their source via fusimotor action. Most fusimotor axons are γ-motoneurons exclusively innervating spindles. A minority are β-fibres (α-motoneurons that innervate spindle intrafusal muscle fibres and skeletal muscle fibres). The way the CNS controls γ-motoneurons in real life has been debated ever since the first microneurographic recordings in humans (Hagbarth & Vallbo, 1968). These showed that spindle afferent firing was correlated to the electromyogram (EMG) activity of the parent muscles, suggesting α–γ coactivation. Unfortunately, it has never been possible to record directly from the small γ-axons, so their activity has always been inferred from the behaviour of spindle afferents. Recordings from spindle afferents in awake monkeys and cats indicated not only the independence of γ control, but also task- and context-dependent activation, also known as 'fusimotor set' (Prochazka *et al.* 1985).

Fusimotor action is of two types, dynamic (γ_d or β_d), which increases the stretch sensitivity of muscle spindle primary (group Ia) afferents, and static (γ_s or β_s), which increases Ia background firing rate while *reducing* stretch sensitivity (Hulliger, 1984). Strangely enough, Kakuda & Nagaoka's (1998) study (this issue of *The Journal of Physiology*) is the first to differentiate dynamic and static fusimotor effects on the discharge of Ia afferents in humans. They report a 50/50 split into afferents with predominantly dynamic or predominantly static effects.

Figures 2 and 4 in Kakuda & Nagaoka (1998) show that the inferences drawn regarding γ action are in line with established spindle properties. Weak static action can masquerade as dynamic action for small stretches (Hulliger *et al.* 1985) and if we compare the scatterplots in Fig. 4 of Kakuda & Nagaoka (1998) with those of Brown *et al.* (1965) it does appear that fusimotor action was weak. If we accept that the movements were large enough to avoid this problem, the 50/50 split into dynamic and static effects indicates that fusimotor action was of mixed type, but one might then expect most spindles to show mixed effects, given that two to three dynamic and five to seven static fusimotor fibres innervate a typical spindle and can influence its Ia afferent(s). The low slopes in the scatterplots do suggest mixed action rather than a clear dichotomy.

A striking feature in this and other microneurographic studies is the low background Ia firing rate (< 20 impulses s^{-1}) and the small changes in rate attributed to γ action (< 30 impulses s^{-1}). In cats, background rates of 75–80 impulses s^{-1} are typical in locomotion; and stretch-evoked responses of 200–500 impulses s^{-1} often occur when limb movements are imposed, a context that often evokes strong γ_d effects. Are human and cat spindles fundamentally different? Not as far as we know from their histology or from experiments on isolated human tissue (Hulliger, 1984). Perhaps the differences in firing rate are related to the behaviours studied. Human subjects are instructed to relax and to make small, slow movements of individual joints to avoid dislodging the microelectrode. In similar movements in cats, spindle firing rates are also low. Higher firing rates are nearly always associated with whole-limb or whole-body movements. Cats are wary creatures and when brought into the laboratory, their readiness to respond is variable and thus their γ_d set may fluctuate more than in humans who can rationalize the situation. The question of whether human spindles are subject to fusimotor set in daily life therefore remains unresolved.

Human spindle firing is usually conspicuously linked to EMG activity, suggesting tight α–γ coactivation; there is little evidence of independent γ activity, even when sought (Kakuda *et al.* 1996). Kakuda & Nagaoka's (1998) results support α linkage of static and dynamic fusimotor action, though β mediation of these effects cannot be ruled out. In contrast, in awake cats, spindle firing is conspicuously correlated to changes in muscle length and behavioural context rather than EMG. Why is this so? First, it is important to affirm the clear evidence for some α–γ coactivation in cats. Numerous studies indicate that one type of γ-motoneuron may be coactivated with α-motoneurons while the other type is tonically active (Gottlieb & Taylor, 1983; Murphy *et al.* 1984). Recent mathematical modelling, in which Ia firing was resolved into velocity, displacement and α-linked components, detected significant α-fusimotor coactivation in muscles strongly active during gait (Prochazka & Gorassini, 1998).

The modelling also highlights the importance of the velocity of muscle length changes. In the step cycle, cat hamstrings stretch at 180 mm s^{-1}. The predicted Ia response to this is $4{\cdot}3 \times \text{velocity}^{0{\cdot}6} = 97$ impulses s^{-1} (Prochazka & Gorassini, 1998). Compare this to the α-linked component predicted for a 50% maximal contraction: 25 impulses s^{-1}. To put this into a microneurographic perspective, suppose a joint moves through 90 deg and an associated muscle changes length by 0·2 rest lengths. To match the 1·8 rest lengths s^{-1} of cat hamstrings mentioned above, the joint would have to move at $1{\cdot}8/0{\cdot}2 \times 90$ deg $s^{-1} = 324$ deg s^{-1}. This is nearly 20 times the angular velocity used by Kakuda & Nagaoka (1998) (17 deg s^{-1}) for which the predicted Ia rate is only 10 impulses s^{-1}, in line with the actual data.

The point of all of this is that microneurography, generally involving slow contractions, provides ideal conditions for the expression of the α-linked components of γ action. In cat locomotion, muscles change length at much higher velocities and this dominates Ia responses. In reality the only unexplained differences are the larger background firing rates in animals and the lack of any striking γ_d set in humans. Perhaps the latter only occurs in very demanding situations. Ultimately the only way to resolve these issues is to record from human spindles or γ-motoneurons in a wide range of unrestricted movements and contexts. In the meantime, Kakuda & Nagaoka's (1998) study provides the first demonstration of separate static and dynamic fusimotor action in human subjects and as such it is an important landmark.

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