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by **Ragnar Granit**

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Breaking down open doors. I think that Roland is breaking down open doors in wanting to prove that proprioceptive impulses can reach consciousness. This was shown in excellent papers by von Frey (1914, 1915, *op. cit.*, 1917/18, and 1926). Roland mentions two of them, but one should also explain that von Frey obtained virtually the same results in studies on human subjects with resected joints, anesthetized joints as well as with severed skin nerves in the moving finger. The experiments of Renqvist cited by Roland also seem to me conclusive for the existence of conscious proprioceptive information.

The Brindley-Merton (1960) experiment on eye movements is, I think, nullified by the experiment of Skavenski (1971) showing that the position of the eye can be perceived in a darkroom when controlled movements are introduced in a sensible manner.

Illusions, like those of Loeb (1890) and Charpentier (see Flowrnoy, 1894), cannot be understood at all on any perception-of-motor-innervation theory.

In my book (1977) I have indicated my basic standpoint to be that the brain is sophisticated enough to perceive consciously whatever information it may need to perceive that way. Normally we do not bother wasting consciousness on largely automatized motor acts, but create the correct situation, as in all the experiments that I have mentioned, and the brain is up to it! Conscious awareness is the supreme executive for purposive responses to the environment.

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by **Peter Grigg**

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On the attribution of a functional role to joint afferent neurons. The article deals with sensory phenomena that are mediated by muscle and tendon receptors. Information about joint receptors is obtained only indirectly in that no effects were observed pursuant to their anesthesia. There is discussion of joint afferents, however, and of the role they might play in kinaesthesia. Although the paper does not deal directly with the properties of joint afferents, it is important that references to their properties, cited in an important paper, should reflect a current understanding of their role. In that regard, joint afferent neurons have been consistently referred to in the paper as being detectors of joint angle. This is a view that is not consistent with the current state of the literature, since most joint afferent neurons have been shown not to discharge at positions that joints commonly occupy.

The works of Skoglund (1956 *op. cit.*) and Boyd and Roberts (1953) are cited as examples that demonstrate that discharge in joint afferents can serve as a signal for joint angle. However, Skoglund's findings of joint afferents that discharge at intermediate joint angles have not been confirmed (Burgess and Clark, 1969 *op. cit.*; Clark, 1975; Clark and Burgess, 1975 *op. cit.*; Grigg, 1975 *op. cit.*; Grigg, 1976). Boyd and Roberts (1953 *op. cit.*) also

described knee joint afferents that discharged at intermediate joint angles. Their results, however, can be attributed to tension in the quadriceps muscles under the conditions of their experiment (Grigg, 1975).

There seems to be no disagreement that most knee joint afferents discharge only at extreme joint angles, a finding that Skoglund (1956 *op. cit.*) himself reports. Rather, the question is the extent to which joint afferents can contribute to position sense at intermediate joint angles. Clark and Burgess (1975 *op. cit.*), in an exhaustive search of lateral, medial, and posterior articular nerves (LAN, MAN, and PAN) failed to find more than 1.5% of MAN afferents and 6.5% of PAN afferents that discharge at intermediate angles of the knee. Further, of the PAN afferents that discharged at intermediate angles, 78% appeared from the popliteus muscle that were contained within the PAN. Ferrell (1977) reported that there are on the average, four afferents in the PAN that discharge at intermediate angles. Furthermore, the sense of joint position in the hip (Grigg, Finerman, and Riley, 1973) and finger (Cross and McCloskey, 1973 *op. cit.*) have been shown not to be altered by capsulectomy and replacement of joint surfaces.

The correct attribution of a role for joint afferents should incorporate the findings that joint afferents discharge (a) when the joint is rotated into an extreme displacement (Skoglund, 1956; Burgess and Clark, 1969; Clark and Burgess, 1975; Clark, 1975; Grigg, 1975; Millar, 1973 *oper. cit.*) or (b) when capsular tension is increased by contractions of muscles inserting into the capsule (Grigg, 1975; Grigg, 1976; Millar, 1973), or (c) when pressure is applied to the joint capsule (Clark, 1975). In the case of the PAN, discharges in most afferents appear to be directly related to capsular tension (Grigg, 1975). Tension in the posterior capsule is developed in extreme extensions (Grigg, 1975; Lavigne, 1974), and may be increased by axial or abductive rotations, or by contractions of certain muscles. In the case of the MAN, discharge in some afferents is observed with extreme rotations, although capsular pressure is the best stimulus for most afferents (Clark, 1975). These observations led Clark (1975) to suggest a role for joint afferents as mediators of "deep pressure" sensations.

The properties of joint afferents recorded in freely moving, unanesthetized cats (Loeb, Bak, and Duysens, 1977 and this Commentary) fully confirm the findings cited above for knee joints and, if anything, stress the lack of a joint position signal in afferents. Primate knee joint afferents (Grigg and Greenspan, 1977) have been shown to be virtually identical to those in cats.

It should be pointed out that the above findings reflect, primarily, observations that have been made on knee and elbow (Millar, 1973) joints. Findings from costovertebral (Godwin-Austen, 1969) and hip (Carli, Farabollini and Fontani, 1975) joints have indicated that full-range receptors exist in those joints. Therefore, it may not be possible to produce a single statement about the general properties of joint afferents, across joints.

In summary, joint afferent neurons may not be considered to be simple detectors of joint angles. In knee and elbow joints, some information about joint angles is contained within the discharge of some afferents. However, this information relates only to joint angles at and around the limits of movement of the joint where the capsule is stretched and is resisting further joint rotation. Further a given discharge rate in an afferent can be diagnostic of several positions of the joint in different axes of movement. In some neurons, any information about joint position is confounded by the effects of muscular tension. Furthermore, since there is substantial hysteresis in the discharge of capsular afferents (Grigg and Greenspan, 1977; McCall, et al., 1974) any information about joint position is further confounded by the effects of the previous history of the sensory ending.

I reiterate that this commentary is directed at the framework within which Roland's work is interpreted rather than at the work itself. My purpose is to prevent the reader from forming either incorrect views or, worse yet, simplistic views of the role played by joint afferent neurons.

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