

## FROM THE ARCHIVES

### The anatomy and physiology of cutaneous sensibility: a critical review. By FMR Walshe. *Brain* 1942; 65; 48–112

The quarterly issue of *Brain* for March 1942 contains only three papers. One is a review, not reporting original research, written by the editor, Dr FMR (Francis) Walshe (1885–1973). Walshe was an astute observer on how the nervous system works but not an experimentalist. He went to Oxford after the Great War intending to work with (Sir) Charles Sherrington (1857–1952) but found himself not well suited to laboratory work. Walshe wrote his critique of protopathic and epicritic sensation in 1921 and showed it to his neurosurgical colleague at University College Hospital, Wilfred Trotter (1872–1939), who advised against publication while (Sir) Henry Head (1861–1940) was living. The minutes of meetings of the Board of Management of the Guarantors of *Brain* indicate that copy was understandably short during World War II. Therefore, when Head died with Parkinson's disease on 8 October 1940, all inhibitions were removed and the review was processed for publication.

Prior to the work of Head, the study of sensation had depended on physiological and morphological descriptions of sensory end organs and their connections; and on anatomical and clinical accounts of nerve injuries. (WHR) Rivers (1864–1922) and Head used regeneration from surgical injury to study the physiology of cutaneous sensory function (A human experiment in nerve division. *Brain* 1908: 31; 323–450). 'In seeking to generalize from his observations, [Head] came to postulate the existence of a double system of cutaneous sensory nerves and end-organs to which he gave the now familiar names of the protopathic and epicritic systems...in addition...the structures deep to the skin have their own sensory nerve supply. The peripheral afferent nervous system consists, therefore, of three fibre systems'. Rivers and Head argued that epicritic sensation provides an increasingly refined set of functions superimposed on the more primitive protopathic system. Later work with (George) Riddoch (1888–1947) extended the epicritic–protopathic concept to function of the spinal cord; and Rivers adopted the protopathic concept in his formulation of primitive instincts and the genesis of psychoneuroses in *Instinct and the Unconscious* (1920). Head made no attempt to ascertain whether or not the skin actually contains the anatomical structures needed to support his ideas, but concluded that these must exist in order to account for the physiological phenomena. (Sir) Thomas Lewis (1881–1945) fell into much the same trap in his work on the 'nocifensor system of nerves'. Conversely, anatomical structures that actually exist are sufficient

to account for the earlier and 'more extensive' work of Trotter. Head's theory depends on anatomical evolution as the basis for altered function. But, for Walshe, there has been very little evolutionary change in structure of the peripheral nervous system. Rather, it is the increasing differentiation and integration of function based on existing structures within the central nervous system that leads to sensory sophistication; or, in Sherringtonian terms, a bringing together through a 'central clearing house' that provides 'better liaison between the old senses'. Walshe plans to deconstruct Head's theory by showing that the facts do not sit comfortably with general principles of physiology and biology; and through failure to identify the putative purely protopathic creature needed to substantiate his formulation within the animal taxa.

Walshe restates the observations on which Head and Rivers based their conceptual formulation of sensation: deep sensibility to moving stimuli and pressure; protopathic sensibility responsive to pain and extremes of temperature, ungraded and with a high physiological threshold that makes it vulnerable to erroneous referral; and epicritic sensibility to touch and intermediate temperatures, having wider unit distribution but low threshold and the capacity for accurate localization and discrimination (see *Brain* 2009: 132; 2903–5). Since recovery is faster and better distributed for protopathic than epicritic sensation, injury and regeneration leave some areas of skin with protopathic sensation only. Later these areas more faithfully report sophisticated sensory stimuli (Fig. 1). But 'that the primary modes of cutaneous sensibility should be regarded as being dealt with by the nervous system in this discrepant manner suggests that the exigencies of hypothesis have borne too hardly on the facts'. Now Walshe proceeds to dismantle the entire edifice of Head's concept of how sensation is processed within the central nervous system. Head postulates two processes, 'specific combination' and 'selective inhibition', dependent on two centres, the thalamus and the sensory cerebral cortex, to which the former is subservient. But how peripheral and central sensory mechanisms, devoid of any specified anatomical substrates, and these two brain centres interact is 'nowhere clearly formulated'. Indeed, Rivers and Head each offer somewhat different formulations in their subsequent writings. For Walshe, 'the process of specific combination is based on a concept that later work has shown to be untenable'. Specific inhibition loses all meaning when the protopathic and epicritic peripheral impulses

<b>Pain:</b>	<b>Punctate end-organs (pain spots)</b>	...	...	<b>protopathic</b>		
<b>Thermal Sensibility</b>	<b>Punctate end-organs</b>	{	<b>heat spots</b>	...	...	<b>protopathic</b>
			<b>cold spots</b>	...	...	
	<b>Non-punctate end-apparatus of unspecified nature</b>	...	...	...	...	<b>epicritic</b>
<b>Touch:</b>	<b>Punctate end-organs (touch spots)</b>	...	...	<b>both epicritic and protopathic</b>		

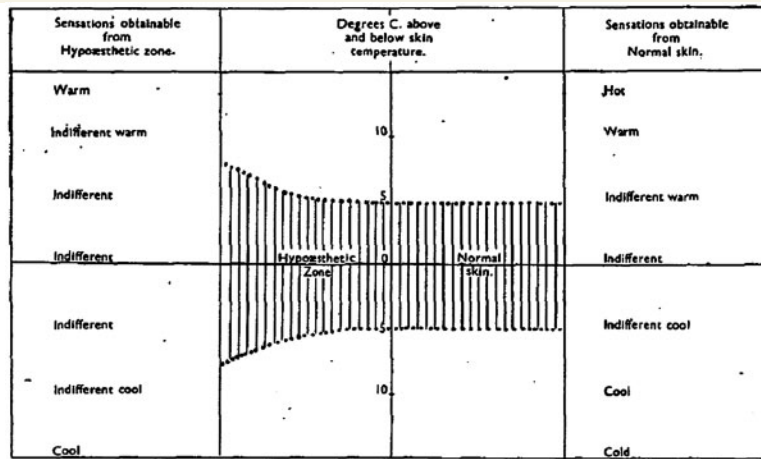
**Figure 1** An arrangement explaining how an end organ can subserve separate modes of sensibility; adapted from the work of Rivers and Head (1908).

reach the same central pathways for conduction of posture, temperature, pain, touch, single spot localization and two-point discrimination: 'we have four different accounts of a single process, and the reader begins to become aware of the insuperable difficulties introduced into Head's theory by the postulation of a dual peripheral sensory mechanism'. While one can conceptualize the differences between crude touch and ability to localize and distinguish points, it makes no sense to conclude that these exist as separate entities that have evolved distinct mechanisms for transmission within the central nervous system: 'the notion of pathways for localization or for discrimination are in the same category as that for pathways for truth or beauty, and are but figments of the observer's mind'. Rather, sensation depends on integrated sensory experience not the mode of sensibility; and this has to occur at a cerebral level. The clinical cases that Head uses to support his thesis are unconvincing; and his conclusions are 'incredible'. At best, epicritic control of protopathic sensibility, for which Head makes no provision, is a metaphor for cortical dominance over thalamic sensibility. Not content with the 'fatal embarrassment' of Head's formulation, and failing to find any validation of the experimental observations by others, Walshe considers even the observations on which it is based to be wrong. 'His theory... must therefore be rejected on factual as well as on theoretical grounds'.

Now Walshe turns to the writings of (John) Hughlings Jackson (1835–1911) to account for the residual sensation following nerve injury and recovery that forms the core observation on which Head's erroneous concept is based; and the notion of lesions resulting in dissolution of function with the emergence of both negative and positive symptoms. But dissolution, reduction to a lower level of evolution, does not imply that such states necessarily characterize the physiological properties of primitive nervous systems. On this, Head is ambiguous claiming at different times that lesions release primitive functions that reveal their original state, and elsewhere that sensations reappear after injury in a form 'which has never existed in phylogenetic history'. And Walshe scolds Head with an acerbic quote relating to hypothesis and truth from Karl Pearson's (1857–1936) *Grammar of Science* (1892). On the existence of the mythical creature endowed only with a protopathic nervous system, such a beast even if it 'could take steps... to propagate its bewildered kind... could have no survival value for on receipt of a stimulus which it could not localize, from a stimulating agent whose nature it had no means of discovering... could respond only by curling up and micturating'. No more need be said of 'a foundation so fantastic'. And, in fact,

organisms such as the polyp *Corymorpha* seem to display splendid properties of epicritic sensibility: 'nowhere in nature do we find a nervous system... comparable with the "protopathic" system of Head and Rivers (*sic*)'. Unlike Head, who relied on the subjective reporting of a single observer (i.e. himself), others (especially Trotter: *J Physiol* 1909: 38; 134–246; and *J Psychol Neurol* 1913: 20; 102–150) have performed identical studies on series of cases; used more extensive means of observation; and reported very different results. They find that, following nerve section, there is an outer hyperaesthetic zone with diminished intensity of sensation to touch, pain and temperature [appreciation of which first alters through widening of the normal range within which there is indifference to change ( $\pm 5^\circ\text{C}$ )] merging with a central area within which these modalities are lost altogether, or have much increased thresholds, but with the appreciation of pressure preserved (Fig. 2). Regeneration is characterized by peripheral reference, variously located, and intensification of the response, which imparts an abnormally vivid quality to sensations despite the raised threshold for their appreciation. Peripheral reference is considered to reflect increased excitability of the relatively unprotected regenerating nerve fibre to constant irritation by the surrounding subliminal stimuli. Head's proposition that the appreciation of pain is dependent on protopathic high-threshold sensation—ignoring the generic threats to tissue integrity of sharp, mechanical, thermal and chemical injury—when its physiological function is to signal impending harm rather than register that damage has already occurred makes no more sense than does the suggestion that distinct systems exist, each with different thresholds, for touch and the localization and discrimination of points. Even if the ideas of Head and Trotter are apparently in conflict, (Edwin Garrigues) Boring (1886–1968), influenced in his thinking more by (Jules) Bernstein (1839–1917) than the Jacksonian philosophy on which Head depends, has settled the matter in favour of Trotter (*Quarterly Journal of Experimental Physiology* 1916: 10; 1–95): 'in short, it may be said that no observer has been able to confirm the essential facts upon which Head's hypothesis rests'.

But the study of injury and regeneration is not the way to understand normal function. Is there a sensory equivalent to Sherrington's motor unit made up of the motoneuron and more than 150 dependent muscle fibres; and might this be made up from all sensory end-organs innervated by a single dorsal root nerve fibre? If so (even in its simplest form, and ignoring the unlikely possibility that a strict one-to-one relationship exists between a single nerve fibre and each end organ) the sensory unit

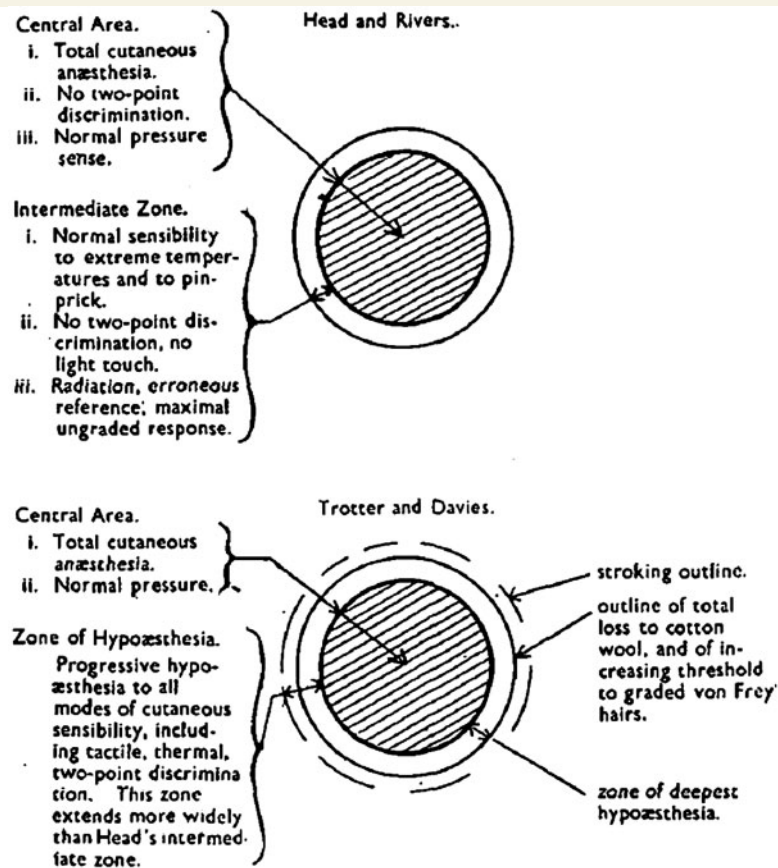


**Figure 2** Changes in appreciation of temperature in the context of nerve injury. Adapted from the writings of Trotter and Davies (see text).

will have three dimensions: touch and its various components; deep pressure and the awareness of displacement; and the combination of pain and temperature. Technology has provided a means, not available to Head or Trotter, for observing the electrical properties of nerve conduction—rhythmic, all-or-none, and with a refractory period, each component varying in threshold and the ensuing sequence of impulses—reflecting the sensory activities of end organs and nerve fibres. Many recent observations support the concept of the sensory unit in which activity in one part involves change and electrical activity in all others. The quality of sensation is characterized by distinct electrophysiological signatures. These are further modified by intrinsic properties of the nerve fibre. To this must be added the concept of the compound action potential that indicates the simultaneous activity of many nerve fibres (and hence sensory units) in response to a stimulus that may be diffuse and involves several qualitatively complex sensory elements (Fig. 3). Aligning the concept of differences in firing imprinted by properties of the nerve fibre with observations on the compound action potential suggests that the initial A response ( $\alpha$ ,  $\beta$  and  $\gamma$  components) depends on large, rapidly conducting fibres with a low threshold for excitability; the long drawn-out C wave represents small, slowly conducting fibres; and the B wave is intermediate. Assigning function by showing the rate at which each is blocked by cocaine shows a hierarchy of mechanical deformation (touch, pressure and postural sensibility: A wave); vibration (B wave); and warmth, pain and cold (C fibres): 'the four primary modes of cutaneous sensibility combined with the sensory impulses received from deep somatic structures, afford support for the view that all the complex sensations experienced can be adequately accounted for as a central integration or fusion of simpler primary ones'. And Sarah Tower (*nk*) has concluded, from work on the cornea, that 'the sensory receptor...is a unit, activity in any part of which affects the whole...the...sensory mechanism [is] an aggregate of units and not...a continuum', a state of affairs that Walshe considers accurately to reflect arrangements in all sensory systems.

'Where there is no structure there can be no function'. Across many species, but most developed in the monkey and man, sensory nerve bundles branch to form a deep and superficial plexus made up of myelinated and non-myelinated fibres. Each end organ receives dual innervation and at least one accessory connection; and each nerve fibre contacts many end organs. The amount of skin served by each varies, generally and topographically. Localization of any sensation results from the massed arrangement of the individual end organs and the multiple innervations of each group. The specificity of sensation lies in the spatial and temporal features of the impulse volley triggered in afferent fibres by the complex patterns of end-organ stimulation. As to what happens in the spinal cord, no better authority is to be found than Sherrington's account of sensation and the nervous system in Schafer's *Text-book of Physiology* (1900: volume 2; pp 783–1025; see *Brain* 2010: 133; 2173–2175). His concept of the prepotent reflex, one that obtains control of other reflex paths and effector organs when subject to multiple peripheral stimuli, extends usefully to pain, the threshold and quality of which are proportionate and appropriate to its protective function. Conversely, 'Head's theory of the morphological constitution of the afferent nervous system is invalid, and... Jackson's doctrine of release of function has proved singularly disappointing as a generalization of the observed facts of sensory loss from lesions of the nervous system... Head's general theory is fatally handicapped... by a fallacious notion of the structure of the peripheral mechanisms of cutaneous sensibility... it succumbs to the danger that always besets abstract thinking; that of confusing thoughts with things'... 'there are insuperable objections to Lewis's interpretation of his observations'; whereas, in not falling into the trap of failing to consider the underlying anatomical basis for any proposed function, the work of Trotter and (Herbert Henry) Woollard (1889–1939) is, in contrast, rigorous and exemplary.

Walshe reprinted 'The anatomy and physiology of cutaneous sensibility: a critical review' as the first essay in his collection of *Critical Studies in Neurology* (1948). The foreword reflects on the



**Figure 3** Changes in appreciation of temperature, pain and touch in the context of nerve injury. Adapted from the writings of Rivers and Head; and Trotter and Davies (see text).

'function of criticism in medicine' and regrets the subjugation of medicine and physiology as natural philosophy in the wake of technology and empirical fact. He asks that the essays be considered as contributing fresh generalizations and an integration of diverse material that provide new patterns not in accord with those designed by the original authors whose work is 'criticized'. Integration and synthesis must accompany the unrelenting accumulation of new facts. 'Science [as] measurement... has become a thought-cramping obsession... and a long and bloodless caravan of equations plodding across the desert pages of some journal between small and infrequent oases of words... no one can tell... whither in the kingdom of ordered knowledge the caravan is bound'. Neurology has suffered its share of deficiency in critical thought. Observation is selection and requires direction from hypothesis. For Hughlings Jackson, the multitude of facts had to be organized into knowledge. For Trotter, critical thought was needed in neurology to deal with 'the mysterious viability of the false'. On journals, Walshe is especially clear—these being

repositories of obsolete lumber indiscriminately and slavishly rehashed for the massive omnibus tomes that constitute the modern textbooks that no student should be asked to bear. Walshe expects that digesting his selection of critical thoughts will make students of neurology 'more gourmets than gourmands'. Wilfrid Trotter did well to persuade Francis Walshe to desist from publishing his decapitation of epicritic and protopathic sensation in the lifetime of Sir Henry Head. But beyond Walshe's comprehensive annihilation, lie issues relating to the anatomy and physiology of peripheral nerve subserving crude and more integrated sensations that still merit publication, even in this particular 'repository of obsolete lumber' (edited, in turn, by Head and Walshe), as the work of India Morrison and colleagues in the present issue makes clear (page 1116).

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