QUALITATIVE DIFFERENCE OF SPINAL REFLEX CORRESPONDING WITH QUALITATIVE DIF-FERENCE OF CUTANEOUS STIMULUS. BY C. S. SHERRINGTON, M.A., M.D., F.R.S.

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QUALITATIVE differences between spinal reflexes provoked from the skin are usually distinguished only in so far as dependent on differences in the regional *locus* of their initiation. The experimentalist has in general to be content to tacitly treat these skin reflexes as of a single kind. But the variety of species of sensation elicitable from the skin suggests that possibly different reflex motor reactions attach to the different species of end-organs undoubtedly coexisting in one and the same skin field. The different kinds of end-organ belonging to one and the same cutaneous region may possess reflex spinal connections differing *inter se*. That this is really the case is indicated by the following observations undertaken in examination of the question.

I. In the "spinal" dog (e.g. after exsection of a short piece, a segment, from the posterior cervical region of the cord) if the skin underneath and between the toe-pads and cushion of the hind-foot be pressed or stretched, a sudden forcible extension of the limb is evoked. This is especially the case if at the time of stimulation the limb be resting flexed at hip and knee. I have called this reflex the "direct extension reflex¹." The extensor movement is brief and ample, and resembles the sharp extension of the spinal frog's leg, of which tracings were furnished in a previous paper².

It is obvious that such a movement, helpful as contributory to progression, would on the contrary be harmful in response to certain other possible stimuli to the foot. Suppose a thorn lying below the foot and applied so as to prick it underneath. If there then ensued the extensor movement that as above described ensues when broad pressure

¹ Proc. Roy. Soc. LXVI. p. 66, 1899; and this Journal, XXIX. p. 67.

² This Journal, XIII. Pl. XXIII. Figs. 4 and 5. 1892.

is applied, the consequence would be a further wounding of the foot by the reflex movement of the leg itself. The foot would be driven forcibly upon the offending point. Observation shows that in fact a prick of the pad-region evokes not extension but flexion of the limb. And the reflex effect of the prick is typical of the reflex effect produced by application to the *planta* of *harmful* stimuli in general. In result the foot is withdrawn from the offending stimulus. Instead of wounding itself further it escapes from the threatened wounding.

Thus in the case of the under-surface of the hind-foot two stimuli of different quality evoke respectively two movements of exactly opposite sense. Two different sets of afferent nerves belonging to this part must therefore be directly connected with respectively two opposed elements of the muscular organisation of the part. Or probably it would be a truer expression of the relation to say that each of the two sets of afferents is connected with both flexor and extensor musculature, but that the one set primarily acts in a pressor manner upon extensor neurones, and in an inhibitory manner on flexor neurones, while the other set acts conversely in a pressor manner upon flexor neurones, and in an inhibitory on extensor neurones.

As to the quality of the nerve-endings involved in each case, the nerve-endings stimulated by the prick lie undoubtedly superficially, for a light prick suffices. Neither mere touch nor cold nor warmth (unless amounting to injurious heat) evokes the reaction. Heat sufficient to threaten injury to the skin does however quickly and regularly, like the prick, evoke the flexor movement. It is fair to infer that the species of nerve-ending excited is that which may be termed the nocicipient, and certainly that division of it which lies in the more superficial layers of the skin.

I have elsewhere put forward a view that there has been evolved in the skin "a special sense of its own injuries¹." There is considerable evidence that the skin is provided with a set of nerve-endings whose specific office it is to be amenable to stimuli that do the skin injury, stimuli that in continuing to act would injure it still further. These nerve-endings when still connected with the sensorium (using that term simply to mean the neural machinery to which consciousness is adjunct) on excitation evoke skin pain. They are in that respect algesic. After their disconnection from the sensorium by spinal transection they still possess spinal connection with large fields of musculature. The reactions they then evoke being devoid of psychical feature the term

¹ Text-book of Physiology, edit. by Schäfer, 11. Art. "Skin and Common Sensation." 1900. algesic becomes inappropriate for them. But harmfulness still remains the characteristic of the stimuli by which they are provocable. For physiological reference therefore they are it seems to me both on this ground and on others which need not be entered upon here, preferably termed nocicipient, a name which has the advantage of greater objectivity.

The other species of nerve-ending, namely that excited by the broad pressure about the pads and cushion and eliciting the "direct extension reflex," is more difficult to identify. Separation of the toe-pads one from another or from the plantar cushion so as to stretch or squeeze one or the other is often a very effective mode of stimulation. The reflex very often ensues on removal of such pressure or tension. Although sometimes the pressure or tension applied must affect the small tendons, ligaments, or joints of the foot I feel satisfied that the reflex often ensues when the application of the stimulus is really confined to the skin, including however the deepest layers of that organ. The pressure and tension requisite in this stimulus seem to resemble what must occur when the limb supports the weight of the animal as it steps. The relief of this pressure and tension, often even more than the application of it, appears to excite the reflex. This suggests that the reflex normally ensues on some change of pressure and tension in the planta occurring towards the latter part of the performance of a step in locomotion.

Applications of either cold, warmth, heat, or of chemical reagents are ineffectual *per se* to evoke the reflex: nocuous mechanical stimuli are also inefficient. But the form of stimulus adequate is nevertheless of mechanical quality, of a kind that may fairly be described as pressure and tension rather deeply applied. Of terms in ordinary use "*deep touch*" might be the least inappropriate.

Applied therefore to the dog's *planta* broad harmless pressure on the one hand and surface damage on the other both readily evoke reflex movements of the whole limb, and the movement evoked in the one case is totally different from the movement evoked in the other.

II. One of the most striking reflexes in the "spinal" dog is the "scratch" reflex. This is a "skin reflex," *i.e.* it is excited by stimulation of the skin. It is however not every stimulus to the skin that can provoke it. In the large reflexigenous field of skin whence it can be evoked¹ various kinds of stimuli can be applied without eliciting any trace of the reflex.

To examine evidence to this effect it is best to work with the skin carefully and cleanly shaved. It is on the shaved skin only that some of the following

¹ Sherrington and Laslett. This Journal, xxix. p. 64.

points can be demonstrated. The application of certain forms of stimuli experimentally through the hairy coat is unsatisfactory. But the existence of a hairy coat in no way essentially alters the problem or the argument.

The finger-tips or the whole hand can be applied to the skin, pitting it, exerting strong pressure upon it and doubtless applying mechanical stimulation to the nerve-endings in it throughout its depth, and yet no scratch-reflex is produced. The skin thus firmly pressed upon can be moved to and fro over the subcutaneous tissue and its deep surface thus rubbed over and against underlying structures soft or hard, and yet this fails to evoke the reflex. If a fold of skin either thin or thick be gathered up between thumb and fingers and then the two layers composing the fold be compressed and, further still, be rubbed freely against one another by their deep apposed surfaces, the scratch-reflex is nevertheless not evoked. Not only is mechanical stimulation in these conditions applied to the deep layer of the skin but the stimulation is applied successively to adjacent fresh areas of the deep layers, and, as can be shown otherwise, successive spatial summation is an adjuvant of great potency in regard to stimuli exciting the "scratch" reflex.

But the reflex is obtained at once if a finger-tip be lightly moved along the skin surface. To draw a pencil point along the surface is even more effective. These stimuli that effectively evoke the reflex press so lightly as to cause very little deformation at all of the skin surface. The difference between the character and efficacy of these stimuli and those mentioned in the previous paragraph is demonstrable in various striking ways. Two may be sufficient to cite here. A rigid ring, such as a bracelet or a large curtain-pole-ring, is applied to the skin, pressed on it, and while pressed upon it moved freely, carrying with it the skin over the subcutaneous tissue; no trace of the scratch-reflex is evoked. But let pencil point or finger-tip be moved over the surface of the skin surrounded by the ring the scratch-reflex is then provoked forthwith. Again, while the fingers by rubbing over the surface of the skin are exciting a vigorous scratch-reflex let them be pressed more against its surface; they then cease to move over its surface, but instead press into it, squeeze all its layers and carry the area to which they are immediately applied with them, rubbing its deep surface over underlying tissue, stretching the skin immediately behind and wrinkling that immediately in front. On this change from superficial to deep stimulation the scratch-reflex at once ceases.

That the nerve-endings which evoke this reflex lie therefore exclusively quite close to the skin surface seems clear. I find further that ablation of the surface of the skin to a depth of 6 mm. abolishes the reflex from the area so treated. The ablated sheet of skin need not include the deepest ends of the hair follicles in order to secure this abolition of the reflex.

When such a surface is made it is obvious that the nerve-fibres belonging to the removed *nerve-endings* must remain, and must, when the surface is fresh, lie exposed. It is noteworthy that of all the stimuli applied none is able to excite the reflex *through* these. The same phenomenon is met in the case of the deep moving pressures on the skin which, as mentioned above, fail to excite the reflex. In such cases, as explained above, the surface stimulation is not a moving one, but the deep stimulation is, and must, one would think, affect the nervefibres passing downward from the overlying surface end-organs that under moving "touches" excite the reflex. Yet no reflex is evoked. Both phenomena, though paradoxical in appearance, remarkably confirm the rule insisted on by Marshall Hall, that spinal reflexes are far more easily excited by stimulation of end-organs than by stimulation of the nerve-fibres conducting from the end-organs.

As to the form of stimulation adequate for these end-organs exciting the scratch-reflex the observations just mentioned show that mechanical stimuli are competent. Such mechanical stimuli as these would, we can hardly doubt, did the condition of the animal allow—that is, were consciousness still adjunct to this region of its skin—provoke psychical "touches." I feel similar stimuli applied to my own skin as "moving touches." Hence it seems fair to conclude that among the species of cutaneous end-organs competent to evoke this reflex in the dog are those of "surface touch," the analogue of those that psychologically examined in man yield evidence of "stereognostic touch."

This set of end-organs, provoking the scratch-reflex in response to purely tactual stimuli, is distributed in close relation to hairs. Evidence of this is as follows. (1) Punctiform stimuli on the shaven skin applied at a hair or hair group—the hairs frequently lie in triads—or just "windward" of a hair, excite the reflex, while elsewhere they fail or are less effective. (2) The threshold value of the stimulus in a given skin area rises after shaving it. This rise is of two-fold character, (a) *immediate*, (β) *late*. The threshold value for a stigmatic touch exciting the reflex by a v. Frey bristle being *e.g.* 60 mgrm. prior to cutting the hairs rises to *e.g.* 520 mgrm. directly after the shaving, although the mechanical stimulation of the shaving itself favours and facilitates (*bahnung*) the reflex. This is the "immediate" blunting. If the skin

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area be kept shaven, gradually in the course of a few weeks ensues a further rise of the threshold values. The difference of facility of the reflex from a shoulder shaved for the first time and that kept shaven for 3 weeks is marked: the reflex is much less easy to obtain in the latter. The presence of these tactual levers, harbouring no doubt some parasitic life, and constantly subjecting their particular nerve-endings to some stimulation or another, seems necessary for the maintenance of the full biotonus-to use Verworn's expressive term-of the reflex arcs which execute the scratch-reflex: (3) The peculiar efficacy of the moving touch as compared with the stationary touch in the provocation of the reflex applies both to the shaven and to the unshaven skin. The finger-tip simply pressed on the skin hardly evokes the reflex, but does so directly it moves along the skin. The moving touch acts more effectively on the hairs and hair stumps; and movement against the hairs is somewhat more effective than movement with the hairs. (4) Depilation of a skin area practically abolishes the capacity of the area to initiate the scratch-reflex. In the process of depilation the plucking out of a hair not unfrequently itself excites the reflex.

It is noteworthy however that to pull on a hair, or even on a little group of hairs, usually fails to excite the scratch-reflex. That mode of stimulation of the hair-nerves is of course not "normal." It is not improbable that the *tactual* apparatus of the hair follicle is not excitable by that kind of application of stimulus. Also it must be remembered that the nerve-endings associated with the hair follicles are considered by some observers to yield sensations sui generis, and distinct from tactual proper. The peculiar tickling sensations evoked by light stimulation of the hairlets of the human skin were by Noischewski and Ossipow¹, working in Bechterew's clinique, found to be well developed in various skin areas where "touch" was not especially fine. The neck, shoulder, back and sides of the trunk, namely a region corresponding with that which is reflexigenous for the dog's "scratchreflex," are specially mentioned by these observers as yielding strong tickling sensations sui generis under light mechanical stimuli applied to the hairlets. V. Frey² has, as is well known, demonstrated the great

¹ Noischewski, Gesellschaft der Aerzte, Dünaburg (Dwinsk) April 2, and November 23, 1896; Ossipow and Noischewski, Gesellschaft der Aerzte, Petersburg, March, 1898; Bechterew, Neurolog. Centralblatt XXII. p. 1032. November, 1898.

² "Beitr. z. Sinnesphysiol. d. Haut," Ber. d. k. Sächs. Gesells. d. Wissensch. z. Leipzig. Math.-phys. Classe. 1894, 1895.

lowering of threshold for mechanical stimuli to the skin which the hairlets effect.

On the other hand, the foregoing shows that the *deep* skin nerveendings are incompetent to evoke the scratch-reflex. Next arises the question, "among the superficial cutaneous nerve-endings are those peculiar to the hairs the only species efficient?" I have tried various "warm" and "cold" stimuli and find them ineffective for the purpose. I conclude that neither warmth nor cold are per se adequate. But early in the investigation I was struck by the efficacy of dragging along the surface a scratching point. This stimulus seems often more effective than the areally far larger stimulus of a moving finger-tip; it is obvious that the former's efficacy may be due to its having not only tangible but noxious quality. It may stimulate nocicipient endings as well as purely tangocipient. Repeated light pricks seem similarly more effective than repeated simple stigmatic touches.

To test this possibility I have had recourse to combination of noxious stimulation with stimulation otherwise per se insufficient. Thus, as has been shown above, a steady pressure applied on one skin area, even large, does not evoke the reflex, even though it be severe. But if a small fold of skin be severely compressed, a short outburst of the reflex may be evoked. The mechanical stimulus is then of obviously noxious kind, and that the reflex is excited through nocicipient end-organs is indicated by its non-appearance when the same mechanical stimulus is applied with intensity insufficient to make it acutely harmful. Again, a warm metal plate one centimeter square and one millimeter thick applied to the skin evokes no trace of the scratch-reflex if applied with a temperature of 65° or less. But let it have when applied a temperature of 85° or more and the reflex is at once vigorously evoked. In order to altogether eradicate tangible quality from the stimulus I have also employed the heat beam as in previous observations¹. The radiation from a good source appropriately collected and applied focally to the skin of the reflexigenous area suffices, if not merely "warm" but "hot" (to the hand), to at once provoke the "scratch"-reflex. I conclude therefore that among the superficial nerve-endings in the skin the nocicipient as well as those merely of the hairs are competent to elicit the reflex, but that the "cold" and "warmth" end-organs are not competent.

Over a large area therefore hair nerve-endings and nocicipient

¹ This Journal, xxvII. p. 360. 1902.

nerve-endings of the skin-surface are physiologically distinguished from the pure "cold" and "warmth" endings and from all the deep cutaneous end-organs by the fact that the two former sets, in contradistinction to all the latter, are spinally so connected with the musculature as to induce under irritation (simulating that caused by parasites) a movement of grooming of the skin itself and of its hairy coat.

Conclusion.

The foregoing observations demonstrate that in the dog different kinds of nerve-endings situate in one and the same cutaneous field possess reflex spinal connections differing wholly *inter se.* For discrimination between certain sets of end-organs in the skin there are in fact available not only psychological criteria involving processes of sense, but data purely physiological with characteristics given in tensions of the musculature.