SOME NOTES ON THE PHYSIOLOGY OF THE NERVOUS SYSTEM OF THE FRESHWATER CRAYFISH (Astacus fluviatilis)[1]. By JAMES WARD, M.A., *Trinity College, Cambridge.*

(*From the Physiological Laboratory, Cambridge.*)

THE experiments in the course of which the following notes were made, consisted mainly in severing by means of a fine sharp hook (1) one, or (2) both of the supra-œsophageal commissures, or (3) the sub-œsophageal commissures, or (4) in dividing the supra-œsophageal ganglion longitudinally. The chief difficulty to overcome was the excessive bleeding sure to ensue if the circulatory apparatus was at all seriously injured. It was found best to scrape away the surface of the carapace with a graver's tool so that the hook could be inserted gently and guided in the direction required. In several experiments the hook, before inserting it, was first dipped in a strong solution of ferric perchloride, and with good results so far as the bleeding was concerned; but the salt sometimes found its way into the tissues and its use was therefore abandoned. The great point was to know accurately where the parts to be severed lay, and this knowledge a little practice ensured. It seems needless therefore to describe in detail the mode of operation: it may suffice to mention that it was found convenient to extemporize a crayfish-holder, which afforded amongst others this advantage, that one could find one's bearings in operating with the needle much better than when holding the crayfish in the hand.

The plan pursued was to perform the same operation on several crayfish in succession, each being marked with a separate number and all kept in running water till the shock was over, when they were taken out one by one and placed in an observing tray and their behaviour noted. Some died the same day, and of these no notes were

[1] A short account of these has already appeared in the *Proceedings of the Royal Society*, No. 194, 1879. The only earlier observations on the subject known to the writer are:—Vulpian, *Physiologie du Système Nerveux*, pp. 780 ff.; Lemoine, *Annales des Sciences Naturelles*, 1868, T. ix., pp. 100 ff.; and Yung, *Comptes Rendus* for Feb. 17th, 1879, pp. 347 ff.

taken: the greater number lived for weeks and many for months, some even casting their shells successfully. The good ones among the dead were placed in spirits and carefully examined to see if they had really suffered all that had been proposed for them; and when it turned out that the operation on a particular individual had been a failure or imperfect, his protocols were of course ignored. It was thought better to run some risk of not really effecting the operation intended than to injure the animal past recovery by laying the commissures bare so as to make certain of their severance; for on the former plan the worst evil was that trouble might occasionally be taken for nothing, while in the latter there was every danger of getting no reliable fact at all, certainly the most interesting would have been lost altogether.

I. Division of one supra-œsophageal commissure destroyed in many ways the symmetry of the animal's form and movements. The abdominal rings appeared to be more loosely articulated on the injured, and drawn more closely together on the sound side of the body; the effect being to make the longer axis convex from the former and concave from the latter aspect. This difference was very marked in the tail-fin; for while the two appendages on the uninjured side continued spread out in the normal manner, like a fan, in the plane of the telson, those on the side of the injury more or less overlapped and drooped from their place of insertion like broken limbs. The want of symmetry just described was most conspicuous when the animal was in motion, and especially when flapping the abdomen: it sometimes disappeared during perfect rest; and disappeared in two cases all but entirely when the nervous connexion between the first and second abdominal segments was completely severed.

In walking the unmutilated crayfish sometimes goes forward, keeping its abdomen extended, sometimes backwards, with the abdomen flexed; it prefers the latter mode when alarmed, and can change it instantly into a swimming movement, in which it shoots rapidly backwards by alternately half extending and then sharply flexing its abdomen with the tail-fin expanded. This last form of progression was altogether absent in most cases under the present rubric: indeed, as a rule, the power over the abdomen was so far lost that the animal when placed on its back had much difficulty in turning: a thing the sound crayfish can do with a single stroke of its tail fin.

Very few of these crayfishes ever went straight; their course forwards, the abdomen being extended, was a curve bending away from

the injured side, and when backing, the abdomen being then usually flexed, they worked round the side of the lesion. But there was a still further want of symmetry, which may help in part to explain this bias. In walking forwards these animals made much more use of the chelæ than they would naturally have done; but instead of planting them both at an equal distance from the median line, the chela of the injured side was bent in till it touched this line, while the other chela diverged at an appreciable angle from it, that is to say when the right commissure was cut the chelæ, which should both have pointed forwards, were each of them directed towards some position on the animals' left; and *vice versa*, the left commissure being cut. Their gait was also abnormal; generally they flopped forwards bringing their chelæ down upon the table with a sharp rap as if they were top-heavy, and sometimes they "wabbled" from side to side.

When turned over on their backs they invariably began to struggle violently with their legs and chelæ to right themselves. At such times a small piece of food placed within the grasp of any of the chelate limbs was usually seized and produced a singular but momentary confusion in the conduct (if the term may be allowed) of the member holding it. Its first impulse seemed to be to thrust the morsel into the mouth, and this was actually done in a few cases—being, as will presently appear, a pretty sure sign that the animal was no longer *compos mentis*. The usual upshot was either that the food was dropped again or that the limb, still holding the morsel, went on swinging like the other limbs, the claws of which were empty. In one case the attempt was made to recover with a pair of forceps a piece which was being swung about in this fashion; whereupon it was promptly stuffed into the mouth and swallowed. No clear difference in the pinch of the two chelæ was perceptible, though the movements of that on the injured side were sometimes feebler, as indeed were the movements of the legs on that side too. But the antenna and eyestalk of this side were always much enfeebled: it was sometimes impossible to get any indication that they were sensitive. The disabled antenna was laid back along the body: the uninjured one alone being waved about as the animal walked. The eye-stalk on the injured side was more protruded and directed less to the front than its fellow.

II. Division of both supra-œsophageal commissures. So long as the highest ganglia are connected with the rest of the (ganglionic) chain by a single commissure, there is no lack of spontaneity and

purpose in the movements of the crayfish: he seeks out food for himself, persists in his efforts to recover from an uncomfortable position, and unless forcibly confined will make his escape from too narrow quarters. But with the section of the second commissure everything of this kind disappears, save that occasionally the antennæ are waved about in the normal fashion though much more feebly. The crayfish so treated were often found next day on their backs and perfectly still, or with only their swimmerets in motion, but still oftener with most of their limbs engaged in a peculiar and monotonous rhythmic swing, to be more fully described presently. A slight disturbance however, such as stirring the water, at once changed all this and brought on two different kinds of movements which might be called "feeding" and "preening" movements respectively. In the feeding movements the two pairs of chelate legs took the chief part: the outstretched limbs being wildly waved about, the pincers grasping eagerly at everything or nothing, sometimes seizing one of the hinder limbs and dragging it towards the mouth; often being snapped together without any apparent reason and inserted empty within the gape of the maxillipedes. The preening movements were the especial function of the last pair of legs, and consisted in an incessant scratching with the terminal hook or dactylopodite of various regions of the sterna, the swimmerets and the tail-fin—the last being the part most constantly attended to. The chelate legs did not occupy themselves with this work except when the parts were specially irritated, and then all four pairs would begin to preen and search about the place affected.

After a time, if there was no fresh disturbance, all these purposeful movements were replaced by the "rhythmic swing," though they would sometimes break out again in the middle of it without apparent cause. The full rhythmic swing was performed by the posterior and second pair of maxillipedes—and possibly other masticatory organs, but not by the mandibles—by the chelæ and the first three pairs of legs, very seldom by the fourth pair. The chelæ however sometimes remained still, and occasionally also the maxillipedes. But whatever were the limbs in motion they all swung together, each moving as a whole and in perfect *tempo*, those of one side swinging forwards while those opposite swung backwards, the limbs coming gradually to rest and a momentary pause intervening between each swing. If the animal were made to lie over towards one side so that the limbs on that side were confined the swing still continued on the other side where the limbs remained free: in a single case a unilateral swing was frequent though both sides were free.

This rhythmic swing often lasted for hours without intermission, but usually subsided at length till a new disturbance brought the animal into action, or the rhythmic motions would break out again to all appearance spontaneously.

Whether at rest, or however occupied, the chelate legs, the chelæ and the posterior maxillipedes were at once excited to more or less concerted action the moment any one of them was touched with a morsel of food, a paper pill, a chip of wood, a tiny stone, or the like. If this were gently rubbed against the dactylopodite of either chela it was seized, usually pretty promptly, and the chela began somewhat slowly to bend towards the maxillipedes: the other chela executing perceptibly later the same movement. The posterior maxillipedes were stretched forwards to the utmost so as to meet the approaching chela; but in this the chelate legs usually outstripped them, secured the morsel, and pushed it into the mouth or, more accurately, within the gape of the maxillipedes. The chelæ, however, often loosed the food too soon, but sometimes, on the other hand, did not slacken their hold at all, the chelate legs trying in vain to wrest the prize from them. If the posterior maxillipedes were touched by the piece first, the terminal joints were at once folded down on the rest like the fingers upon the palm, the action being repeated many times while the maxillipedes themselves were waving about in quest of the exciting fragment. At the same time the chelæ moved towards the spot, and the chelate legs came to their assistance as before. Any small object once within the grasp of these last was placed with surprising promptness and certainty in the mouth (*i.e.* well within the gape of the maxillipedes and directly over the mandibles) and there left.

During actual or attempted mastication the feeding movements were suspended: in at least one case the rhythmic swing used to take their place till they set in wilder than ever when the food was swallowed. But as a rule so long as there was food in the mouth the first pair of chelate legs kept guard with open pincers just over it as if ready to seize any falling crumbs or to still the efforts of struggling prey. Immediately any particular act of mastication was over, as the morsel was on the point of being swallowed, there regularly ensued a peculiar wiping motion of the second pair of maxillipedes, the effect of which was manifestly to cleanse the surface of the mandibles after contact with food. And it was singular to observe how, simultaneously with this movement, as if it were the recognised signal for a renewed forage, the chelate legs ceased their waiting and set up at once a vigorous search for fresh

booty. When a piece of food was placed in the mouth large enough to occupy the masticatory apparatus for a minute or so it was possible by touching the small chelæ with fragments loosely held between a pair of forceps to charge all four chelate legs with a new supply some time before the mouth was empty. But till it was empty, though the fragments were instantly grasped, not a limb would move towards it. Still they did not wait with that composure which was usual when they waited empty-handed: in two cases in which the experiment was tried the legs holding food while the mouth was full appeared as if seized by a sort of palsy or possessed by a spirit of fussiness. A similar agitation of the limbs was also noted in crayfish that were near dying when food was placed in the small chelæ. If it was too long before the mouth was empty the piece instead of being held till then was simply dropped: but more than once it was noticed that a chelate leg which had lost an earlier chance of delivering up its morsel held it till the pieces put into the mouth by the others were eaten and then at last came forward with its own at the end of all.

As soon as what was seized as food got within the gape of the mandibles, if not before, there was usually ample evidence of taste or discrimination, and what was then ejected was instantly brushed away by the second pair of maxillipedes in the way already described. But neither the chelate limbs nor the posterior maxillipedes manifested any selective power at all: putrid flesh, pieces of blotting-paper soaked in acid, tannin, or oil of cloves were crowded on to the mouth, and, however often rejected, pushed back again with a most hearty zeal. A favourite subject for this treatment was the animal's own antennae, and it was droll to observe the persistence with which these were tucked into the mouth despite their continuous writhing.

Placed upon their feet on the table these crayfish assumed an attitude and behaviour very different from those of a sound animal. The latter stands with its abdomen either extended or closely flexed, and only raises its body sufficiently to clear the ground: its ambulatory legs bend upwards to the carpopodite, and then turn sharply downwards, looking something like the legs of a cricket, and insuring that its centre of gravity shall be as low as possible. But after the supra-œsophageal ganglion is isolated, the animal seems intent on getting its centre of gravity as high as it can: its ambulatory legs are straightened out, and the body lifted up as if upon stilts, so that the abdomen, which is half flexed, *i.e.* turned down at right angles to the line of the cephalo-thorax, barely touches the ground with the tail-fin. The chelæ were in some

cases confined rigidly to the vertical plane, and bent inwards so as to touch the ground about the median line, and just under the animal's rostrum, causing the body to topple over the moment the ambulatory legs attempted to move forwards: more frequently they were not folded across at all, but each was extended forwards and allowed to rest on the ground on its own side; and whenever the chelæ could take this less constrained position, they could also be used for locomotion. But always, whether locomotion was possible or not, the animal remained a good half-minute at rest in this stilted attitude without venturing a step. Not that its legs were motionless however: far from it. The two fore-pairs betook themselves at once to feeding movements, grasping about the table as far as they could reach, and lifting to the mouth whatever small object they chanced to find; whilst the last pair would busy themselves either preening the abdomen, or rubbing against the third pair as the legs of flies are rubbed together. During all this the antennæ were waved feebly to and fro. At length when the animal might be supposed to have collected itself, there was an attempt at locomotion. The success of this attempt depended chiefly, as has been said, upon the use that could be made of the chelæ. Where they were not folded like a stumbling-block across the animal's path, but could be lifted out of the way, they were slowly raised high in the air and extended, to be then with most ludicrous deliberateness, and in a tottering fashion, lowered to the ground again: the whole action having an air of caution that might suggest to an overlooker that the animal suffered badly from corns. The movements of the ambulatory legs were in most cases tolerably well co-ordinated, though slow and feeble: but the great want was the power to keep equilibrium, the difficulty of doing this being of course increased by the elevation of the centre of gravity. By extending the abdomen and pressing the animal close to the table, so as to make it assume as nearly as possible the normal attitude, animals that were otherwise unable to stir without rolling over could often be got to take two or three steps: but in such cases, by the end of the third step or thereabouts, the stilted attitude was resumed and the animal fell. In the pauses between the steps the ambulatory legs were nearly sure to resume their more special functions of preening or prehension, and the legs of the third pair in particular had an odd trick of turning straight round for a moment and pointing directly upwards over the animal's back—probably it is their function to preen the sides of the carapace. When put upon their feet in the water (instead of out of the water on a table) these crayfish had not such a strikingly stilted attitude, and

did not as a rule attempt to walk, but began either feeding or preening movements, or falling over a little to one side set up the rhythmic swing instead.

III. Division of both commissures behind the first post-oral ganglion. The crayfish subjected to this operation used their antennæ more frequently and vigorously than those last described: their eye-stalks too were oftener seen to move. When left undisturbed, they frequently made no movement except occasionally to lash their antennæ from side to side a few times or work their swimmerets. It was a very rare thing for them to resort to feeding movements spontaneously, but they occupied themselves with preening very much more than the others did, and in this all four pairs often took part. The rhythmic swing was not infrequent in the maxillipedes, but was seldom seen, and then only for a moment, in the other members. In one case the first post-oral ganglion was completely isolated by dividing the commissures connecting it with the supra-œsophageal ganglion, and after this the rhythmic swing of the posterior maxillipedes became very marked.

In these crayfish, as might be expected, there was an absence of all *rapport* between the maxillipedes and the chelate limbs in the prehension of food: it was possible, when the animal was motionless or engaged in preening, to feed it by means of the maxillipedes without arousing or diverting the other members; but contact of food with the chelæ at once excited the chelate legs under this just as under the last head. But when these last had secured their object they seemed to have forgotten the way to the mouth, sometimes missing their aim and catching against the base of the chelæ or the side of the maxillipedes, and then rubbing the piece up and down these parts as if it were a sponge and they needed washing; more frequently they persisted in poking the morsel under one of the maxillipedes from its outer side instead of dropping it between the two and directly over the mouth; and when at last they chanced to reach the right spot they did not at once loose their hold. It is further noteworthy that the fact of the mouth being already full, made no difference to their efforts to crowd into it everything they got, which they did, not turn about, but all together. Struggles too of an extraordinary kind were constantly occurring between them, when two or more happened to close on the same piece of meat, and sometimes lasted several minutes, the piece being eventually torn to shreds, and most of it strewn about the bottom of the tank. At first

sight these "struggles" appeared to be purposeful, but this is almost certainly not the case: for the normal procedure of the crayfish in eating strips of meat is rather to close the mandibles upon one end of it, and the hard bristled edges of the posterior maxillipedes upon the other, and then by depressing both maxillipedes together to tear the piece in two. Moreover it happened not unfrequently that when two chelate legs met over the mouth one would carry off what the other had just brought, and perhaps begin rubbing it up and down the base of one of the chelæ, the two seeming to differ as to where the mouth really was. And not only were the antennæ frequently pounced upon, but sometimes one or other of the hinder legs was tugged towards the mouth as well. These crayfish were extremely apt to reject even good food, brushing it away by means of the second pair of maxillipedes with most obstinate sulkiness; but in two cases out of three in which the experiment was tried this sulkiness disappeared on dividing the supra-œsophageal commissures, the very food that had been refused before the operation being eaten within an hour after it. In the third case there was possibly some injury from the operation, the animal dying in little more than a day later, whereas one of the others lived on for a month without being seen to refuse food again.

When placed upon their feet the present crayfish assumed a position almost the antithesis of that of their predecessors, and differing in the opposite extreme from that of the uninjured animal. The back was curved just as it is in the dead crayfish, so that as the rostrum and tail-fin rested on the ground, there was barely room for the legs to move when they were not, as they often were, doubled up under the body: the chelæ were sprawled out helplessly on either side. The only attempt at locomotion they could make was to raise their cephalo-thorax by depressing the posterior maxillipedes, and this movement they would repeat two or three times a minute till they were exhausted, the antennæ being waved vigorously all the while. Sometimes, when lifted up in this manner, instead of falling flat again they toppled over on to their backs, still however continuing the movement of the maxillipedes, which might be felt to press against the finger with surprising force. In striking contrast with the strength of the posterior maxillipedes was the weakness of the chelæ: not only were these powerless for locomotion, they were much enfeebled as pincers too. The ambulatory legs paid absolutely no regard to the animal's efforts to move; the two hind pairs were either rubbed together (fly-fashion), or occupied in preening: only the front pairs grasped about the ground

seizing small stones and trying to put them in the mouth. When lying upon their backs, the abdomen was often half, or more than half flexed, so that the feet could reach all parts of the tail-fin, but the power of instantly flexing the abdomen was lost, though several times manifested in crayfish with the commissures below the œsophagus intact.

IV. Longitudinal division of the supra-œsophageal ganglion. This is a difficult operation to perform at all satisfactorily, and the remarks that follow are made on the strength of only three cases, one of these however extending over a fortnight, and the other over three months.

In all three there were very marked "circus movements" both forwards and backwards. All adopted the stilted position described under II. when placed on the table, but the abdomen instead of being bent sharply downwards was alternately elevated to the utmost, and then depressed, and sometimes retained curved rigidly backwards for a minute or more. And as the chelæ were at the same time crossed in the perpendicular plane through the rostrum the animal could be set firmly on its head without falling till the abdomen was flexed again. These animals had considerable power of maintaining equilibrium, and were active in the water. Their ambulatory legs were always obedient to the impulse to walk, and never, as in the cases last described, betook themselves to feeding or preening movements at such times. They were strangely irritable, flapping the abdomen frantically if it were touched, and fighting together whenever they met.

It may not be out of place now to invite attention to certain points which these experiments seem to prove, and to some questions they seem fairly to suggest.

The effects of the unilateral division of the commissures shew perhaps that there is no decussation of the longitudinal fibres in the nervous system of the crayfish (unless this occurs within the supra-œsophageal ganglion itself).

The fact that the antennæ are waved about when the commissures are severed immediately below the supra-œsophageal ganglion is evidence that this ganglion is not identical with the cerebral lobes of vertebrates.

That it is the highest centre however follows from the disappearance of spontaneous activity on the part of the animal as an individual as soon as this ganglion is isolated. Thus food refused before is refused no longer, and taken even when the animal is laid upon

its back; whereas a sound crayfish in this position does nothing but strive to recover his feet: only when utterly exhausted by being turned afresh on his back as often as he gets off it does he begin to act like one without its cephalic ganglion. The power to maintain equilibrium is also lost along with this ganglion as well as the power to inhibit the exuberant activity of the lower centres: those incessant feeding and preening movements are absent so long as it retains even an imperfect connection with the ganglionic chain behind. Further, the use of the abdomen and tail-fin in swimming to all appearance depends on the integrity of this ganglion.

But the second or sub-œsophageal ganglion appears to have functions so nearly equal in importance and so superior to those of the ganglia below as to justify Leydig's comparison of the first two ganglia to a vertebrate brain in which the œsophagus passed between the *crura cerebri*. Possibly the centres of taste or relish are located in this second pair, though this is not certain. There was much in the action and inaction of the mandibles to suggest very considerable independence between the centres for their movements and those for the movements of the maxillipedes. Thus the mandibles in several cases lost the power to move while the maxillipedes continued unaffected, and never at any time participated in the rhythmic swing or feeding movements of these last. It may be then that the mandibular palps and the anterior end of the œsophagus or whatever be the organs discriminating food are connected with the stromato-gastric nerves given off from the œsophageal collar. But at any rate the sub-œsophageal ganglion is the centre *par excellence* for co-ordinating the movements of the limbs. So long as it remains the complex apparatus employed in the prehension of food works perfectly, although often needlessly; and walking too is still possible, whereas without the direction of these ganglia not a step can be taken. When the commissures are divided behind the second thoracic ganglion the animal crawls with extreme difficulty by alternate advances of the chelæ; when they are divided behind the third it gets along alternating both the chelæ and the first pair of legs: the other legs are rucked together in confusion just as all five pairs are, as mentioned under III., when all are divided from the sub-œsophageal ganglion. The rhythmic swing there described is indicative of the subordination of this ganglion to the cephalic ganglion: this swing is possibly analogous to the chorea manifested by the higher animals during certain structural or functional derangements of the supreme centres. Nay, it is not unlikely that in such rhythmic movements we see a relapse to

the only activity possible in a lower stage of development, and that the more complex movements acquired during connection with the later evolved centres of the special senses are, as Hering might say, because the last learned, the first "forgotten." Still the difference already noted between the rhythmic swing of the thoracic limbs and the swing of the swimmerets is, it must be allowed, a difficulty in the way of such an explanation.

In the stilted position assumed when the sub-œsophageal ganglion is deprived of the direction of the anterior pair we have a new difficulty. Why should not the limbs which in the prehension of food execute the appropriate movements in the normal way and yet are controlled by the sub-œsophageal ganglion move in an equally normal fashion when under the conduct of the same centres they are set to walk? Perhaps because these centres have a different part to perform in the two cases. The inability of the chelate legs to aim straight for the mouth may be due simply to the absence of sensory guidance, the motor impulse coming from the lower centres under the stimulus of the object grasped. Leaving this then aside, the only office remaining to the sub-œsophageal in the prehension of food would be that of inhibiting the activity of the chelate limbs till the masticatory apparatus is disengaged. But in locomotion the initiative for each particular limb appears to come from this ganglion: mere contact with the ground does not, and from the nature of the case could not, bring on stepping movements. Nay, even standing at all ceases to be possible without direction from the higher centre. Thus it is probable that the rigid and constrained gait is at bottom traceable to the same cause as the rhythmic swing, to the absence, viz. of the cephalic ganglion in regulating and economising the motor discharges. The difference between the two phenomena, the easy rhythm of the one and the irregular stammering of the other, may be explained, as suggested, by supposing the first to be the more primitive movement and as such independent of the higher centres: children can kick out well lying on their backs before they can crawl when put on "all fours."

The occurrence of the feeding and preening movements in the absence of the two first ganglia is perhaps the most striking point in these experiments. The farce of grasping at nothing and making empty passes to the mouth may have been chiefly due to the solicitation of the gustatory apparatus, since it became so much less frequent when the commissures between the first two thoracic ganglia were divided: but even after this, as soon as the chelate legs were touched, the feeding

movements were almost wilder than ever. Freed from the control of the anterior ganglia these limbs act more like four hungry creatures just aroused by prey than as mere members of one individual. If we assume the first two pairs of ganglia to be homologous with the vertebrate brain and the remaining ganglia to be homologous with the vertebrate spinal cord there is then a remarkable difference between the decapitated crayfish, and say, the decapitated frog. From the latter it is impossible to get any continuous movement at all, to say nothing of such as might almost suggest that some of its members have a life on their own account. But in the decapitated crayfish the feeding movements occurred without extraneous stimulation, and spontaneous preening movements went on at intervals during several weeks. There is thus much less solidarity, a much less perfect consensus, among the parts of the nervous system in the crayfish than in animals higher in the scale of being.

But some of the phenomena described make it probable that at all events some stimulus within the organism but external to the particular centre is more or less necessary to its activity. Thus the antennæ were waved more frequently and more vigorously, and the eye-stalks were oftener in motion, when the supra-œsophageal ganglion remained connected with the sub-œsophageal, than when they were isolated from these as well. So too the diminution in the spontaneous feeding movements after the separation of the above-mentioned ganglion admits of a like explanation; while the increased preening manifest at the same time may be similarly referred to the excitation from the tail-fin region having no longer a counterpoise.

It remains to mention certain experiments which belonging to no particular head have been reserved till now. The swimmerets which were oftener in motion after operation III. than after II. were in either case brought instantly to rest by gently touching the anal region; and not the movements of swimmerets only but the feeding and preening movements were also suspended; and in the cases under II. the movements of the masticatory apparatus as well. But this suspended action was followed, especially in the cases last mentioned, by violent preening movements and by flexure of the abdomen. On the other hand, if the swimmerets were at rest, irritating the anus set them in motion but not so quickly as it stopped them when moving: there was generally time for the abdomen to curl up and for the hind legs to start preening before the swimmerets moved. If two or more abdominal ganglia were isolated by dividing the commissure both anteriorly and posteriorly

the corresponding swimmerets could still be excited for a moment by striking the ventral surface on which they lay: if the abdominal commissure was divided in the middle the swimmerets behind the section could be excited to considerable activity by touching the anus. The anus itself could also be sometimes made to gape rhythmically by gently inserting a seeker into it. Beside their close sympathy with the anal region the swimmerets are also at once affected by any interference with the sexual organs: to touch these excites or inhibits the swimmerets, according as they are already at rest or in action, and leads to a folding of the abdomen. In the male too a single peculiar spasmodic twitch is induced in one of the last pair of legs by touching the generative organ on that side.