Feed-back regulation in *Platynereis dumerilii* Audouin & Milne-Edwards, 1833: a status review

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ABSTRACT

In *Platynereis dumerilii*, gametogenesis and heteronereid transformations, as well as growth and regeneration of posterior parapodial segments, proceed under the endocrine control of presumeably a single hormone, which is produced by and released from the supraoesophageal ganglion. As the universal principle applying to all gonochoric, monotelic species in the family Nereidae investigated so far, this hormone controls postlarval development in a concentration-dependent manner. The juvenile growth-phase and the early stages of gametogenesis are determined by high hormone levels which, simultaneously, prevent precocious maturation and metamorphosis. Decreasing hormone levels correlate with gamete maturation, heteronereid metamorphosis and, on the other hand, with a loss of regenerative capacity. Neither oocyte differentiation beyond the critical stage nor spermiohistogenesis require additional hormone. The decline in hormone concentration in *P. dumerilii* is not based on a brain-autonomous control of hormone production and release but results from a more complex system of exogenous and endogenous factors acting on the cerebral ganglia. Severe amputation of segments in both maturing females and males was, but transection of the nerve cord was not the decisive factor for brain hormone activation. Removal of oocytes, injection of oocytes or of spermatogenic cells into juvenile hosts affect hormonal activity, and juvenile prostomia are inactivated when passaged in maturing males. The results are interpreted in terms of inactivation (or reactivation respectively) of brain hormone activity, caused by humoral feed-back emanating from coelomic cells, probably the germ cells. These findings are similar to but not identical with those concerning brain-body interactions in female *Nereis diversicolor* and *Perinereis cultrifera* . Isolation of a low molecular weight substance has been reported from the latter species, but the retroacting factor(s) in *Platynereis dumerilii* have not yet been analysed yet.

RÉSUMÉ

Revue de la régulation en rétroaction chez *Platynereis dumerilii* Audouin & Milne-Edwards, 1833

Chez *Platynereis dumerilii* la gamétogenèse et la métamorphose hétéronéréidienne, ainsi que la prolifération et la régénération de segments parapodiaux sont conditionnées par l'action d'une hormone élaborée par les ganglions cérébroïdes. Comme principe universel des espèces de Néréidiens à reproduction gonochorique et monotélique, le contrôle

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hormonal du développement postlarvaire s'effectue en fonction de la concentration de l'hormone. La phase juvénile de croissance et le début de la gamétogenèse sont assurées par un taux hormonal élevé, qui, en même temps, inhibe la maturation et l'épitoquie précoce. Le progrès de la gamétogénèse, de la métamorphose et l'arrêt de la régénération postérieure se relient à une diminution progressive de l'activité endocrine. Par contre l'ovogenèse et la spermatogenèse, au delà d'une phase critique, sont achevées même sous des conditions anhormonales. La réduction caractéristique du taux de l'hormone au cours du cycle vital ne résulte pas du contrôle autonome de la synthèse et de la sécrétion par le cerveau lui-même mais ressort d'actions plus complexes de facteurs endogènes et exogènes sur les ganglions cérébroïdes. L'amputation d'un nombre substantiel de segments postérieurs altère le status endocrine des vers mâles et femelles proches de la maturité sexuelle. Néanmoins, la lésion de la chaîne nerveuse ventrale, due à l'opération, n'est évidemment pas la cause de la réactivation endocrine cérébrale que l'on constate. Cependant, l'enlèvement des ovocytes ou l'injection d'ovocytes submatures (ou de cellules spermatogénétiques) dans le coelome des vers juveniles, influence l'activité endocrine du contexte. En plus, des prostomiums prélevés sur des animaux juvéniles subissent une déactivation du cerveau au cours d'un passage dans le coelome des mâles s'approchant de la maturité. Ces effets sont considérés comme le résultat d'une rétroaction humorale sur l'activité endocrine cérébrale provenant vraisemblablement des produits génitaux. L'interdépendance humorale entre le corps et le cerveau constaté chez *Platynereis dumerilii* est comparable, mais n'est pas tout à fait identique à celle observée chez *Nereis diversicolor* et *Perinereis cultrifera*. Une substance provoquant l'arrêt de l'activité hormonale cérébrale a été isolée des ovocytes de la dernière espèce; par contre un facteur analogue n'a pas encore été identifié chez *P. dumerilii*.

INTRODUCTION

Feed-back control means that a controlled system itself is acting back on its own control unit either to maintain or to alter a given physiological state. In the case of endocrine control of sexual maturation in nereid polychaetes, a feed-back phenomenon was first described by DURCHON (1952) in *Perinereis cultrifera*. He discovered that oocytes and associated coelomocytes taken from females approaching maturity ("ovocytes submatures", diameter ≥ 180 µm) and injected into immature males of the same species caused precocious gamete maturation and epitokous transformation. Since DURCHON (1948, 1952) had found out that maturation and epitoky are controlled by an inhibitory hormone originating from the prostomium, he concluded that the submature oocytes released a factor which down-regulated this inhibitory hormone, thus enhancing gamete maturation and heteronereid metamor-phosis. This was the first indication of possible interaction between the endocrine system and the maturing body.

All available data agree with the view that, as an universal principle in nereids, a single hormone, which is produced most probably in neurosecretory cells of the brain, controls postlarval development in a concentration dependant manner. It has been found to be neither species specific nor sex specific, and to work in species with and without epitokous reproductive form.

The present report considers currently available data on the regulation of endocrine activity in *Platynereis dumerilii*, one of the most thoroughly investigated nereid species. The following question is asked: is the brain hormone titer regulated by brain-autonomous control of production and release, or is it determined by a more complex system of exogenous and endogenous factors acting on the neurosecretory ganglia? In particular, I review results of investigations aimed at demonstrating feed-back phenomena during male and female gametogenesis, metamorphosis and regeneration of posterior segments. These findings are discussed and compared with studies bearing on feed-back control in *P. cultrifera* and on brain-body interaction in *Nereis diversicolor* (e.g. PORCHET & CARDON, 1976; PORCHET, 1984; GOLDING, 1987).

DEVELOPMENT OF *PLATYNEREIS DUMERILII*

P. dumerilii, originally described from the Mediterranean and the french Atlantic coast, is a gonochoric, typically monotelic species, which develops a pelagic, epitokous reproductive form. Sex appears to be genetically controlled and the diploid complement of chromosomes was found to be 28 (HANSKE, 1989). The same diploid chromosome number was found also in the sibling species *P. massiliensis* and *P. megalops* (D. JÖRG, Univ. Mainz, pers. comm.). In neither sex are typical gonads present, gametogenesis proceeds in the coelomic fluid. Recently, HANSKE (1989) detected paired, segmental sites at dorsolateral positions, from which small clusters of spermatogonia appear to be proliferated and released into the coelom (but see the findings in *Nereis grubei* by REISH, 1954). Metamorphosis into the reproductive form parallels the final stages of gamete development; the pelagic heteronereis then broadcasts the fully mature eggs and sperm during pheromone controlled nuptial dances

(ZEEK *et al.*, 1988 for review). There is no brood protection; early phases of development, including trochophore and metatrochophore stages, are pelagic. Nectochaeta larvae later start settling and forming tubes on the substratum from secretions of parapodial glands. In laboratory cultures maintained by now standard methods (HAUENSCHILD, 1951), development from fertilized egg to the heteronereis stage is variable and takes from 3 to 12 months with a small proportion of "stragglers" taking up to 18 months (HAUENSCHILD, 1966). Of a total of 635 males 65% reached maturity within 4-8 months (HANSKE, 1989); the same author recorded a similar life-span for females. With its very short life-cycle, correlated with rapid growth and fast regeneration, *P. dumerilii* differs considerably from *P. cultrifera* and *Nereis diversicolor* which require 2-3 years to reach the reproductive status in the field.

ENDOCRINE CONTROL OF POSTLARVAL DEVELOPMENT

Results of the pioneer work by DURCHON (1948, 1952), performed first on male *Nereis irrorata* and *Perinereis cultrifera*, suggested that spermatogenesis and epitokous metamorphosis are controlled by an inhibitory, endocrine factor formed within the prostomium. Using female worms, HAUENSCHILD (1956, 1965, 1966) conducted prostomium amputation experiments on laboratory reared *P. dumerilii*, focussing on gametogenesis, metamorphosis and caudal regeneration. His results largely confirmed DURCHON's observations, but moreover, provided a much more detailed hypothesis of the hormonal control mechanism in this species. He concluded that a single prostomial hormone is responsible for the control of both gametic and somatic development, acting in a concentration dependent manner. The juvenile growth phase and proliferation of germ cells require a high titer of hormone, which inhibits late stages of gametogenesis and epitokous transformations. When oocytes reach diameters of 80-100 µm, a photoperiodically triggered decrease of hormone concentration initiates a new phase of oocyte growth and differentiation, stops the addition of new segments, quènches posterior regeneration, and allows then metamorphosis of somatic tissues. Once the level approaches zero, development of heteronereid swimming setae is completed and oocytes undergo final maturation. The heteronereis then aquires the competence to respond to sex pheromones, i.e. to perform nuptial dances and to shed the gametes soon after it begins to swim. Since absolute hormone concentrations could not be measured, HAUENSCHILD (1965) used arbitrary units and suggested, but did not indicate in his Fig. 19, a logarithmic scale. DURCHON & PORCHET (1971), PORCHET (1973), and SCHROEDER *et al.* (1977) arrived at similar conclusions when studying developing individuals of several species of nereids, despite the fact that the former authors were using an entirely different organ-culture system to assay the hormonal activity of homogenized prostomia (see BERTOUT, 1984 for details of the *N. diversicolor* spermatogenesis assay).

The major drawback of the work discussed herein is that the precise site of production and release of the hormone, its molecular structure, its rate of synthesis and secretion, and its absolute concentrations are not yet known. We must use live prostomia, or homogenates (fresh or lyophilized) as a source of the active compound, and we have to deduce or to determine indirectly relative values of hormone activity (or concentrations respectively) from biological assays based on morphogenic or cytomorphologic criteria.

All recent evidence confirms the view that the hormone concentration in *Platynereis dumerilii* is maximal in juvenile animals and decreases to zero in the heteronereid, and a high level of activity is required to sustain segment formation, to support the proliferation of oogonia and spermatogonia, and to suppress premature maturation and epitoky (HOFMANN, 1975, 1976; SCHIEDGES, 1981; HOFMANN & SCHIEDGES, 1984; MEISEL, 1990). It has been confirmed that growth and regeneration capacity decrease and somatic metamorphosis starts when the hormone level is lowered. However is has become a matter of dispute whether all successive developmental events in somatic tissues and germ cells are directly controlled by specific levels of hormonal activity. HAUENSCHILD (1966) found that oocytes,which had a critical diameter of about 100 µm, completed a morphologically normal oogenesis after the prostomium had been removed. No further hormone supply was required at that stage. On the other hand, implantation of one or two prostomia from juveniles into female recipients with oocytes of diameters larger than 100 µm significantly prolonged the time of survival, but retarded and disturbed both oogenesis and metamorphosis when compared to either decapitated worms or controls. Though oocyte development beyond the critical stage can proceed without continued hormone secretion, the maturing oocytes are still sensitive to altered endocrine conditions (HOFMANN, 1975).

The same type of experiments led to different results when performed on males. Prostomial removal from juveniles caused defective development at the end of which the worm fragments were still lacking major heteronereid characters and did not contain any gametes. Individuals with some small clusters of spermatogonia in the coelom (early spermatogonia cluster I phase) showed a dual response. Whereas metamorphosis was defective in

all cases, the course of spermatogenesis was morphologically normal. None of the stages was omitted but the entire sequence was accelerated ; it took only 12.5 days on the average instead of one to several months to produce mature spermatozoa. If, however, worms were decapitated at the end of the first mitotic proliferation phase (late spermatogonia cluster I phase), not only spermatogenesis but also metamorphosis was accelerated. At this stage 93% of the experimental worms developed normal heteronereid characters (MEISEL, 1990).

Implantation of one to three prostomia from juvenile donors into developing males, from the advanced spermatogonia cluster stage onward, left spermatogenesis unaffected. Differentiation of sperm proceeded at about the normal rate. This is in obvious contrast to the findings in females. On the other hand, heteronereid transformation was strongly affected and disordered by this manipulation of the hormone level, as in the corresponding experiments on female *P. dumerilii* (SCHIEDGES, 1981; HOFMANN & SCHIEDGES, 1984).

Gamete development in both sexes and metamorphic events appear to be strictly coordinated in ontogenesis, but to be experimentally dissociable. Spermatogenesis turns out to be considerably less sensitive to the alteration of endocrine conditions than oogenesis. It is remarkable that development of heteronereid characters can be seriously delayed and disturbed by manipulating the endocrine status even very late in gametogenesis. The sibling species *P. massiliensis*, although morphologically indistinguishable from *P. dumerilii*, has an entirely different, benthic mode of reproduction. These proterandric hermaphrodites do not metamorphose; they deposit, fertilize, and brood the eggs within their tubes. Posterior regeneration was shown to decrease drastically in the absence of the prostomium (CASANOVA, 1955), but no unequivocal proof of brain hormone control of either spermatogenesis or oogenesis could be developed (HAUENSCHILD, 1970; LÜCHT, 1987 for review).

FACTORS AFFECTING THE ENDOCRINE ACTIVITY OF THE BRAIN

ENVIRONMENTAL FACTORS

HAUENSCHILD (1966) demonstrated photoperodic control of swarming periodicity in *P. dumerilii* and has further shown maturation and epitoky to be hormonally governed. He therefore postulated that the synodic or experimentally modified light-dark regime acts via the neuroendocrine pathway. However, no detailed study on light-to-hormone signal conversion is available to prove this hypothesis.

Temperature has been reported to affect hormone gamete-interaction in *N. diversicolor* (DURCHON & PORCHET, 1971), but the influence of temperature on development and endocrine activity has not been studied in *P. dumerilii*.

REGENERATION OF POSTERIOR SEGMENTS

The number of setigers regenerated following amputation of the posterior end is positively correlated with the number of segments removed. As mentioned earlier, at a given level of transection, the number of segments regenerated decreases concomitantly with the progress of gamete maturation and metamorphosis (HAUENSCHILD, 1966; HOFMANN, 1966; SCHIEDGES, 1981; HOFMANN & SCHIEDGES, 1984). HAUENSCHILD (1966) also noticed that in maturing females amputation of a significant number of posterior segments led not only to regeneration but also to retardation of sexual development and to delayed metamorphosis. These results suggest that hormone production has been stimulated, possibly mediated by the injury of the ventral nerve cord (see HOFMANN, 1966 for discussion of earlier work). More detailed investigations in female *P. dumerilii* showed that maturation was delayed and significant regeneration occurred only when about 50 of approximately 70 parapodial segments were removed. Furthermore, the size of the regenerate and the delay in reaching the heteronereis stage decreased as individuals of more advanced stages of sexual development were assayed (HOFMANN, 1975).

In males, the number of segments regenerated and the delay in heteronereid metamorphosis are likewise correlated with the number of segments amputated and with the stage of sexual development. However, spermatogenesis continued unaffected when males from the late spermatogonial stage onward were assayed. In such cases we observed males deprived of all but 20 segments which showed posterior regeneration and significant delay of metamorphosis, but in which spermatogenesis proceeded independently. They contained mature spermatozoa a full three weeks before reaching the heteronereis stage.

The hypothesis that the site of nerve cord lesion causes a position-dependent increase in hormone production and thus determines the course of regeneration and maturation was tested. In males and females at selected stages of development, the ventral nerve cord was excised from segments 20 and 21 (or the circumoesophageal connectives

deleted) prior to amputation of the posterior end behind segment 40 (HOFMANN, 1966, 1975; SCHIEDGES, 1981). The results did not support the assumption that nerve cord injury activates hormone secretion and thus enhances posterior regeneration accordingly. Therefore, stimulation of the neurosecretory cells via the nervous system does not appear to be the decisive control mechanism. There must be other components modulating brain hormone activity by stimulating its production or by temporarily preventing its decrease. Candidates are the developing gametes, the somatic coelomocytes interspersed with the gametes, and various somatic tissues.

FEED-BACK ACTIVITY OF GAMETES AND COELOMOCYTES

When deprived of all but 20 segments, female *P. dumerilii* with oocytes measuring 130-150 µm in diameter regenerated up to 12 segments and survived up to 25 days, whereas those cut behind segment 40 did not form regenerates but transformed into heteronereids within one week, as did the controls. Amputation of about 2/3 of the animals parapodial segments means that the hormone "source" has to serve thereafter only a much smaller part of its "sink". Even at a given, constant production of the factor, a higher concentration may result in the much smaller body and could account for enhanced regeneration and retarded heteronereid development. If one bears in mind that some cells of the "sink" acquire the ability to feed back on and to inhibit the hormone producing cells, cutting off segments involves not only a decrease of the "sink" volume, but also a reduction of the mass of cells feeding back on the hormone source.

DURCHON (1952) suggested that a coelomic factor associated with the oocytes and eleocytes of submature *P. cultrifera* reduced the endocrine activity of the brain in immature recipients injected with gametocytes and coelomocytes.

Several lines of evidence indicate that down-regulating factor(s) exist in *P. dumerilii* as and are major components of developmental control (HOFMANN, 1975; SCHIEDGES, 1981; HOFMANN & SCHIEDGES, 1984; MEISEL, 1990). In these investigations, the number of segments regenerated by males and females at selected stages of development, the time period required to form the heteronereis, or the survival time, were used to determine such effects.

REMOVAL AND INJECTION OF COELOMIC CONTENTS

Removal of oocytes and coelomocytes by stripping following caudal amputation led to enhanced regeneration and to significantly delayed metamorphosis at stages in which regeneration had normally ceased (HOFMANN, 1975). When intact juvenile worms were deprived of all but 40 segments and were injected with the coelomic contents of females with oocytes ranging from 100 to 180 µm in diameter, effects on the recipient's development were observed only when 100 to 120 µm oocytes were injected. Seven out of 15 juvenile recipients started to regenerate but then stopped and transformed into heteronereis within 11 to 17 days, whereas controls took one to several months (HOFMANN, 1975).

Stripping of gonia from males was much more difficult and could not be done quantitatively. The experimentals were apparently affected by the manipulation and did not develop well. This will not be considered further (SCHIEDGES, 1981). Injection of mature spermatozoa and coelomocytes into very young females (oocyte cluster stage) caused accelerated oocyte growth and metamorphosis, and significantly reduced the regeneration of posterior segments. Quite unexpectedly, males at the initial stage of gametogenesis did not respond to sperm injection. On the other hand, juvenile worms, when injected with gonia from spermatocyte/tetrad or tetrad stage donors, metamorphosed much faster than the controls, *i.e.* in only about 62 % of the time. However regeneration was clearly reduced only when the colomic contents of tetrad stage donors was transferred (SCHIEDGES, 1981).

These observations are compatible with the hypothesis that factors, probably stage specific, are associated with gametes and coelomocytes, which influence development by altering the endocrine activity of the brain. Under these premises stripping of the oocytes means removal of the feed-back factor and results in hormone production and, consequently, in enhanced regeneration and delayed metamorphosis. On the other hand, injection of differentiating gametes and coelomocytes adds such factors which then suppress hormone production in the immature host. This would account for their limited regeneration and accelerated epitokous development and maturation.

PROSTOMIUM TRANSFER EXPERIMENTS

Additional evidence for the existence of coelomic factors which feed back on hormone production has been provided by prostomium transfer assays. HAUENSCHILD (1966) found that prostomia taken from maturing females and implanted into decapitated fragments of younger females, exhibited a stronger maturation inhibiting and regeneration promoting activity than they would have *in situ*. He assumed that the different "environment" in the younger recipients had somehow stimulated the activity of the implant. SCHIEDGES (1981) systematically tested the properties of prostomia taken from males at different spermatogenetic stages and transferred to juvenile, decapitated hosts. She noticed that prostomia excised from worms at the spermatocyte cluster stage, the spermatocyte/tetrad stage and at the tetrad stage could be assigned a higher endocrine activity than when tested *in situ*, thus confirming and extending HAUENSCHILD's result.

SCHIEDGES (1981) provided further support through very elegant prostomium passaging experiments performed on *P. dumerilii*. Prostomia excised from immature donors were implanted into male intermediate hosts at different stages of spermatogenesis and were left there for one week. Then the prostomia were excised again and implanted into definitive, immature, decerebrate 40 segment host fragments.

In individuals receiving prostomia which had been passaged in intermediate hosts ranging from the juvenile state to the spermatocyte /tetrad stage there was a slight decline in both numbers of segments regenerated and in survival time, compared to the controls. However a significant decrease occured only in those receiving prostomia which had been passaged through intermediate hosts at the tetrad or sperm stage. This proved that the secretory activity of prostomia is negatively affected when exposed to the coelomic "environment" of maturing males. This influence appears to be stage dependent and to be strongest during the last two spermatogenic stages. Isolation and characterization of factors which exert negative feed-back on endocrine activity and which do not appear to be sex specific, has not yet been attempted in *P. dumerilii*.

FEED-BACK CONTROL OF BRAIN HORMONE ACTIVITY IN OTHER NEREID POLYCHAETES

Extending DURCHON's (1952) earlier work, PORCHET (1967), PORCHET & DURCHON (1968), and PORCHET & CARDON (1972, 1976) studied the effect of maturing oocytes ("ovocytes submatures", diameter $\geq$ 180 µm) injected with their adhering coelomocytes into recipient male and female worms at different stages of development in *P. cultrifera*. In this species, which takes three years to reach sexual maturity, oocyte transfer turned out to cause long-term effects, observed only after many weeks or even months. Injection of submature oocytes into juvenile hosts led to precocious gametogenesis: 93 % of the males produced sperm and also transformed into heteronereids within 110 days. Surprisingly, female recipients underwent only abortive, although accelerated oogenesis but did not metamorphose, in contrast to the findings in *P. dumerili* (HOFMANN, 1975; SCHIEDGES, 1981; HOFMANN & SCHIEDGES, 1984). Injection of coelomic contents was also found to affect posterior regeneration, *i.e.* the number of segments regenerated was negatively correlated with the size of the injected oocytes. After carrying submature oocytes for 50 days, initially juvenile recipients failed to regenerate any segments within a period of 20 days, though controls regenerated an average of 14 segments.

PORCHET & CARDON (1972, 1976) showed that the precocious gametogenesis, epitoky, and inhibition of regeneration, which followed injection of submature oocytes, was not a response to the injection. They demonstrated that the effect is based on a chemical factor, the action of which could only be interpreted in terms of down-regulation of brain hormone activity in the recipient. In separate assays, they examined the biological effect of oocytes, coelomocytes, coelomic fluid, and of extracts of somatic tissues on host animals. They found that the factor causing brain hormone inactivation is associated exclusively with the oocyte fraction. PORCHET & CARDON (1976) purified the factor from an aqueous ethanolic oocyte extract. The compound appears to be a low molecular weight substance which is dialysable, heat labile, resistant to proteolytic enzyme action, and ninhydrine positive. It does not seem to be a peptide, but has been suspected to be a glycoprotein. The feed-back substance is obviously different from the two peptides, B_1 and B_2, also isolated from the coelomic fluid of *P. cultrifera*, which stimulate the final phase of oocyte differentiation (PORCHET *et al.*, 1979).

GOLDING (1967, 1983, 1985, 1987) provided a large body of evidence for humoral brain-body interaction in *N. diversicolor* which corroborates many of the findings and conclusions reported above. *N. diversicolor* reaches maturity in the second or third year of life. It does not develop a pelagic heteronereis but shows an atokous, benthic reproductive form. Gamete maturation is accompanied by the progressive loss of capacity to proliferate and

regenerate posterior segments. As in the other nereid species considered here, decreasing brain hormone levels account for this developmental pattern.

Prostomium passaging experiments involving prostomia from female donors at various stages of oogenesis and using both immature and maturing intermediate hosts, demonstrated that the endocrine activity can be influenced in either direction. Prostomia from maturing donors, known to exhibit only reduced regeneration promoting activity, were apparently reactivated when subjected to repeated intracoelomic conditioning in immature intermediate hosts. On the other hand, deactivation of prostomia was observed after passaging for a prolonged time period in maturing hosts. Deactivation was readily achieved in prostomia excised from donors at later oogenetic stages, but failed to occur in some of those taken from juvenile worms. Furthermore, injection of submature oocytes into immature *N. diversicolor* had a long-term negative effect on regeneration, provided that the injected oocytes did not degenerate. However final oocyte maturation and spawning was not normally observed in these individuals. Thus, submature oocytes can be assigned a brain hormone deactivating influence in *N. diversicolor*, too.

The results of the prostomium passaging experiments can be interpreted, as proposed in *Platynereis dumerilii*, in terms of inhibition and activation of neuroendocrine activity of the respective prostomia, though no information is available on the regulatory mechanism. Although humoral retroaction on brain hormone activity has been demonstrated also in male *P. dumerilii* (SCHIEDGES, 1981; HOFMANN & SCHIEDGES, 1984), no corresponding investigations seem to have been done on male *P. cultrifera* or *Nereis diversicolor*. Feed-back control in oogenesis of *Cirratulus cirratus* (OLIVE, 1973) and in spermatogenesis of *Arenicola marina* (HOWIE, 1984 for review) are well-known examples of retroaction in gametogenesis of polychaetes. They are not related, however, to the system of gamete-brain-soma interaction discussed here for members of the family Nereidae.

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