

Darwin's Ethology and the Expression of the Emotions: Biosemiotics as a Historical Science

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Abstract Because of the reduction of his theory to *The Origin of Species* (1859) and its slogan “descent with modification by means of natural selection”, Darwin's contribution to the study of language is largely overlooked. However, in later works, such as *The Descent of Man and Selection in Relation to Sex* (1871) and *The Expression of the Emotions in Man and Animals* (1872), Darwin develops his theory of language and of signs in general. These considerations are contained within Darwin's ethology, which is different from the theory of instinct of *The Origin* based on natural selection. Respecting the idea of continuity between non-human animals and human beings, the Darwinian animal appears as a hermeneutical subject that constructs its own world and behaves accordingly by taking into account both its structure and the surrounding conditions. Moreover, the Darwinian animal is able to emit both voluntary and involuntary signs that can be recognised as such by the animal or an observer (human or non-human). *The Expression of the Emotions* is dedicated to the study of sign emission, which has to be understood in the context of Darwinian ethology. In this article, I argue that both Darwinian ethology and biosemiotics (represented by the theory of the expression of the emotions) correspond to Saussure's definition of historical sciences. Darwin's ethology and biosemiotics are composed of contingent facts that have to be studied historically.

Keywords Ch. Darwin • F. de Saussure • Ethology • Expression • Emotions • Signs • Biosemiotics

Introduction

Darwin's contribution to the study of language may not appear central to his theory of evolution or to the history of linguistics. Indeed, the English naturalist is sometimes reduced to the author of a single book, *On the Origin of Species* (1859), which is summarised in a slogan: descent with modification by means of natural selection.

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Although the classification of languages is analogous to the classification of species,¹ the origin and development of language is not treated in *The Origin*. The fact that Darwin is not interested in such aspects of language in *The Origin* is not really surprising. Human beings are strategically absent of the book, except for a sentence in its conclusion, probably the most famous understatement of the history of science: “Light will be thrown on the origin of man and his history”.² Moreover, even animal behaviour is practically left untouched in *The Origin*, excepting some considerations in the context of the law of use and disuse and the seventh chapter of the first edition dedicated to instinct.³

Darwin’s silence on human faculties in *The Origin* does not mean that they cannot be explained by means of natural selection. The faculty of language makes no exception, as it is argued by Steven Pinker’s popularisation of such a view in *The Language Instinct* (1994). Darwin’s contribution to the study of language can be easily identified in two closely related books: *The Descent of Man and Selection in Relation to Sex* (1871) and *The Expression of the Emotions in Man and Animals* (1872). With respect to language, both these books directly contradict an adaptationist, neo-Darwinian approach of faculty. More precisely, Darwin is not interested in the faculty of language itself but in its expression through diverse kinds of languages. In other words, Darwin develops a semiotic theory that Sarah Winter justly qualifies as biosemiotics.⁴ In order to explain Darwin’s biosemiotics, which is drastically different from a neo-Darwinian approach to language such as the one defended by Pinker (1994), it is necessary to understand its basis that can be associated with the ethology developed in *The Descent of Man* and *The Expression*.

In order to illustrate the historical and theoretical value of Darwin’s biosemiotics,⁵ I will firstly explain the principles of the ethology developed in *The Descent of Man* and *The Expression*. Secondly, I will illustrate Darwin’s biosemiotics through the analysis of the three principles of expressive movements given in *The Expression*. This study will lead to a Saussurean definition of both the naturalist’s ethology and biosemiotics as historical sciences.

¹Darwin 1859, pp. 422–423; Alter 1999.

²Darwin 1859, p. 488.

³*Ibid.*, pp. 134–139, 207–244.

⁴Winter’s definition of biosemiotics will be applied in this article: “By biosemiotics I mean not only a theory that reads biological systems in semiotic terms but also one that shows how such systems function at all levels through signaling and thus through producing nonlinguistic biological signs” (Winter 2009, p. 130).

⁵While I will adopt Winter’s definition of biosemiotics, I will focus on Darwinian ethology and on its compatibility with Saussure’s epistemology of the science of language, which constitutes an extension of Winter’s work.

Principles of Darwinian Ethology

Although several authors have emphasised the importance of animal behaviour in Darwin's thought,⁶ this subject remains largely unexplored. Two complementary reasons explain why Darwinian ethology has been generally overlooked. First of all, the seventh chapter of *The Origin* seems to reduce most animal behaviour to the complex phenomenon of instinct.⁷ Far from being a hasty solution, Darwin's theory of instinct is subtly articulated and is the result of a long maturation on the subject, the naturalist's path towards the theory of *The Origin* being identifiable in his manuscripts.⁸ Indeed, confronted to the problem of explaining the different structures and behaviour of neuter insects, i.e. insects in a given community that are unable to reproduce, Darwin has to abandon the Lamarckian theory of the heredity of habits, which necessitates direct reproduction.⁹ Using for the first time community selection, Darwin reduces most complex behaviour to the selection of accidental/spontaneous variations that present an advantage for the individual or its community in the context of a general struggle for existence.¹⁰ Given the solution to the question of instinct in the seventh chapter of *The Origin*, it would be superfluous to look for a more developed ethology, especially if this book is considered as a summary of Darwin's thought.

Secondly, the theory of instinct contained in *The Origin* is based on principles that are in line with the natural sciences. By contrast, Darwin's ethology developed in his manuscripts, in *The Descent of Man* and in *The Expression* can be accused of relying on dubious principles and methodology.¹¹ For instance, the laws of heredity used by Darwin in the context of sexual selection are modelled on the hypothesis of pangenesis,¹² while *The Expression* is entirely based on the heredity of habits.¹³

⁶Cf., e.g., Durant 1985; Burkhardt 1985; Richards 1987; Townshend 2009.

⁷Darwin does not give a definition of instinct, which he seems to reduce to an innate tendency to accomplish more or less complex actions in accordance with the external circumstances.

⁸The entries in the *M* and *N* notebooks are numerous, the evolution of Darwin's thought on instinct is also particularly well illustrated in his 1842 *Sketch*, his 1844 *Essay* and his 1856–1858 *Natural Selection*. Cf. Darwin, quoted in Barrett et al. 1987 [2008, pp. 517–596]; Darwin, quoted in F. Darwin 1909, pp. 17–21, 112–132; Darwin, quoted in Stauffer 1975, pp. 466–527. I have treated this issue elsewhere, cf. Thomas 2013.

⁹Richards 1987, pp. 142–152.

¹⁰Darwin 1859, p. 242.

¹¹Cf., e.g., Ghiselin 1969 [2003, pp. 187–213].

¹²The “provisional hypothesis of pangenesis” is Darwin's theory of heredity developed in *The Variation of Animals and Plants under Domestication* (1868). This complex and fascinating theory states that each part of an organism emits gemmules that are transmitted through reproduction. Changes in the organism lead to similar changes in the gemmules and to the possibility of the inheritance of new traits. However, complex rules preclude a systematic heredity of new characters. It has to be noted that the hypothesis of pangenesis can be considered as a theory of reproduction compatible with the heredity of habits. Cf. Darwin 1868, vol. II, pp. 357–432; Ghiselin 1969 [2003, pp. 181–186]; Ruse 1979 [1999, pp. 212–213]; Hodge 1985, pp. 227–237; Endersby 2009, pp. 82–86.

¹³The extensive use of the heredity of habits renders *The Expression* strangely un-Darwinian for readers that consider *The Origin* as a summary of Darwin's thought (cf. Radick 2010).

Moreover, animal behaviour is described through anecdotes and explained in anthropomorphic terms. Both pangenesis and the heredity of habits have been contested by Friedrich Leopold August Weismann's theory of the impermeability between *soma* and *germen* and the development of genetics. Anthropomorphism and anecdotes have been criticised in ethology since Conwy L. Morgan's canon: "In no case is an animal activity to be interpreted in terms of higher psychological processes if it can be fairly interpreted in terms of processes which stand lower in the scale of psychological evolution and development".¹⁴ In sum, Darwinian ethology can be viewed as outdated.¹⁵

In order to attest the historical importance of Darwin's ethology and to recognise its potential usefulness in the study of signs, it is necessary to understand its context of development. Between 1859 and 1871, Darwin's silence on man in *The Origin* has allowed the most diverse extrapolations, such as Herbert Spencer's social Darwinism, William Rathbone Greg and Francis Galton's eugenics or Alfred Russel Wallace's surprising limitation of natural selection to exclude human higher faculties. However, such interpretations do not represent Darwin's theory of man.¹⁶ Prompted by such wrong applications or limitations of natural selection, Darwin chose to end his silence on man, realising his project of writing a treatise on this subject that had been abandoned during his work on the different editions of *The Origin* and *Variations*. More precisely, Darwin wrote *The Descent of Man* in reaction to "The limits of natural selection as applied to man", in which Wallace, the co-discoverer of natural selection who had recently converted to spiritualism, states that natural selection cannot be responsible of the higher faculties of man and that an intelligent force must be reintroduced in evolution.¹⁷ In short, while *The Origin* was written to challenge appeal to independent creation and natural theology, *The Descent of Man* is mostly directed against creative design with a focus on the case of man.

Although *The Descent of Man* rectifies the applications and limitations of natural selection with respect to man, Darwin does not argue for a vision of evolution based uniquely on natural selection. Indeed, the naturalist recognises a certain instance of limitation of natural selection:

Thus a large yet undefined extension may safely be given to the direct and indirect results of natural selection; but I now admit, after reading the essay by Nägeli on plants, and the remarks by various authors with respect to animals, more especially those recently made by Professor Broca, that in the earlier editions of my "Origin of Species" I perhaps attributed too much to the action of natural selection or the survival of the fittest. I have altered the fifth edition of the "Origin" so as to confine my remarks to adaptive changes of structure; but I am convinced, from the light gained during even the last few years, that very many structures which now appear to us useless, will hereafter be proved to be useful, and will therefore come within the range of natural selection. Nevertheless, I did not formerly con-

¹⁴Morgan 1895, p. 53.

¹⁵Ghiselin 1969 [2003, pp. 187–213]; Durant 1985, pp. 291–292, 302–303; Burkhardt 1985, pp. 328, 348–349, 351.

¹⁶Cf. Tort 2010, pp. 63–152.

¹⁷Cf. Wallace 1871, pp. 332–371. Cf. also Kottler 1974 and 1985, pp. 420–421; Richards 1987, pp. 186–187.

sider sufficiently the existence of structures, which, as far as we can at present judge, are neither beneficial nor injurious; and this I believe to be one of the greatest oversights as yet detected in my work. I may be permitted to say [...], that I had two distinct objects in view; firstly, to shew that species had not been separately created, and secondly, that natural selection had been the chief agent of change, though largely aided by the inherited effects of habit, and slightly by the direct action of the surrounding conditions. I was not, however, able to annul the influence of my former belief, then almost universal, that each species had been purposely created; and this led to my tacit assumption that every detail of structure, excepting rudiments, was of some special, though unrecognised, service. Any one with this assumption in his mind would naturally extend too far the action of natural selection, either during past or present times.¹⁸

As a manifesto in favour of transmutationism, *The Origin* is prone to exaggeration. As Darwin emphasises, natural selection is not the only operative principle in evolution. Indeed, as already mentioned in the first edition of 1859, he gave weight to other principles. These principles, such as the heredity of habits or the influence of conditions, complement natural selection in cases in which behaviour lacks adaptive value. Darwin is relatively careful on such non-adaptive characteristics, underlining that an adaptive value could be inaccessible due to the advancement of science. However, the second part of *The Descent of Man*, dedicated to sexual selection and written before the first part,¹⁹ is more radical on this issue. Indeed, sexual selection is not a particular case of natural selection²⁰ but, rather, leads to the development of useless and injurious structures and behaviour. In other words, the observation of animal behaviour, particularly in the context of courtship, makes Darwin open what could be considered as a domain of the useless,²¹ in which non-adaptive and anti-adaptive structures and behaviour can be explained. The domain of the useless, though never identified as such by Darwin, constitutes the naturalist's answer to the arguments against natural selection or its misuse.

Darwin's ethology is directly opposed to Morgan's canon since the naturalist states that "the more the habits of any particular animal are studied by a naturalist, the more he attributes to reason and the less to unlearned instincts".²² This generosity towards animals is opposed to the reduction of animal behaviour to complex instincts in *The Origin*. Persuaded of the continuity between man and other animals, Darwin develops a double argument representing his global ethology: zoomorphic anthropology and anthropomorphic zoology.²³ Every human faculty is identifiable in animals, despite quantitative differences, while animal behaviour can be described and explained by anecdotes related in anthropomorphic terms. Sexual selection is certainly the most pregnant illustration of Darwinian ethology. During courtship, males try to seduce females by singing or displaying their ornaments. Such behaviour is at

¹⁸ Darwin 1874, pp. 61–62.

¹⁹ Burkhardt 1985, pp. 349–350.

²⁰ In other words, Darwin is not a precursor of sociobiology (cf. Mayr 1972, p. 88). For a conciliation between Darwin and sociobiology, cf. Cronin 1991, pp. 113–249.

²¹ The adjective *useless*, although prone to be criticised, is here chosen on purpose as opposed to *useful*, i.e. to advantageous behaviour and structures in the context of the struggle for existence.

²² Darwin 1874, p. 75.

²³ These terms are used as they have been established by Durant (1985).

first conscious but can become an instinct thanks to the heredity of habits.²⁴ Females choose consciously their favourite males by using their sense of beauty. Anthropomorphism reaches its climax in the comparison of such seductive behaviour and human cultural rituals:

With respect to female birds feeling a preference for particular males, we must bear in mind that we can judge of choice being exerted, only by analogy. If an inhabitant of another planet were to behold a number of young rustics at a fair courting a pretty girl, and quarrelling about her like birds at one of their places of assemblage, he would, by the eagerness of the wooers to please her and to display their finery, infer that she had the power of choice. Now with birds, the evidence stands thus; they have acute powers of observation, and they seem to have some taste for the beautiful both in colour and sound. It is certain that the females occasionally exhibit, from unknown causes, the strongest antipathies and preferences for particular males. When the sexes differ in colour or in other ornaments the males with rare exceptions are the more decorated, either permanently or temporarily during the breeding-season. They sedulously display their various ornaments, exert their voices, and perform strange antics in the presence of the females. Even well-armed males, who, it might be thought, would altogether depend for success on the law of battle, are in most cases highly ornamented; and their ornaments have been acquired at the expense of some loss of power. In other cases ornaments have been acquired, at the cost of increased risk from birds and beasts of prey. With various species many individuals of both sexes congregate at the same spot, and their courtship is a prolonged affair. There is even reason to suspect that the males and females within the same district do not always succeed in pleasing each other and pairing.²⁵

At the opposite of Darwin's anthropomorphic account of courtship among animals, Wallace, respecting Morgan's canon, denies both the conscious seductive action of males and the choice exerted by females. According to Wallace, the fittest males develop ornaments thanks to a surplus of energy and are able to captivate females.²⁶ While animal behaviour can be explained by natural selection operating on mechanical variations, human structures and behaviour need the intervention of an intelligent force since they are far too developed in primeval men and savages or are obviously injurious to them to be accounted for by natural selection, which has immediate utility as criterion.²⁷ An ultra-adaptive theory leads Wallace to maintain a discontinuity between animals and man. Darwin softens natural selection, letting the domain of the useless emerge, in order to allow a strict continuity in the animal reign.

The opposition between Wallace's discontinuous theory and Darwin's insistence on continuity is mostly obvious in the account given to the useless and the injurious. Indeed, prefiguring the Baldwinian theory of evolution based on organic selection,²⁸

²⁴Darwin 1874, p. 402. In more modern terms, the epigenetic level, represented by the heredity of habits, is the source of the evolution of behaviour. This explanation of the evolution of behaviour is opposed to the theory of instinct defended in *The Origin*, which would correspond to a genetic account of behaviour.

²⁵*Ibid.*, pp. 420–421.

²⁶Wallace 1889, pp. 268–300.

²⁷Wallace 1871, pp. 332–371 and 1889, pp. 445–478; Kottler 1980 and 1985, pp. 417–425; Cronin 1991, pp. 123–164.

²⁸Baldwin 1896.

Darwin transfers the selective power to the animal in the case of non-adaptive or anti-adaptive structures and behaviour. Not only are females able to choose their mate thanks to high intellectual faculties and aesthetical sense, but also the animals in general can be considered as reacting intelligently to their structure, taking into account their surrounding conditions. For example, female birds that have inherited conspicuous colours, acquired by the males in the context of sexual selection, can intelligently modify their habits of nidification.²⁹ The useless and the injurious can be conserved thanks to the transfer of selective power to the animal. The domain of the useless is ever-expanding and leads to a modification of the definition of natural selection. From the positive and creative principle of the *Origin* that acts on spontaneous variations, natural selection becomes a negative and eliminative principle in *The Descent of Man* due to the transfer of the selective power to the animal. Darwin's insistence on continuity does not simply consist of zoomorphic anthropology, recognising the fact that man is only an animal, but is also based on anthropomorphic zoology, emphasising the mental powers of the entire reign.

The Darwinian animal does not correspond to the animal described by mainstream ethology, which has followed both René Descartes and Conwy L. Morgan's path.³⁰ Indeed, Darwin's animal is not at all a machine deprived of surprises that can be described by an ethogram. On the contrary, the Darwinian animal is always interpreting and constructing its own world influenced by a triple history: phylogenetic, cultural, historical.³¹ The fact that the animal is at the crossroads of three histories is particularly well illustrated by the emission of signs, which is explained in *The Expression* where Darwin considers the semiotic character of the animal. The study of expression, completing Darwin's ethology, has to follow the same principles developed in *The Descent of Man*. In short, understanding the animal consists of considering how and why it constructs its own world as it is.³²

²⁹ Wallace argues that coloration is always under the realm of natural selection. According to him, conspicuous females having the habits of hatching unprotected are eliminated while less conspicuous females are selected. Darwin reverses this process by stating that when females become conspicuous, they alter their habits of nidification. While it could be possible that such new habits are the results of the selection of a spontaneous variation, Darwin's anthropomorphic zoology suggests that such behaviour is the product of intelligence and can become instinctive by the heredity of habits. It has to be noted that this alteration of the hatching habits echoes the acquisition of instinctive fear in *Natural Selection*, which is certainly the best example of the use of the heredity of intelligent habits in Darwin's manuscripts (cf. Darwin, quoted in Stauffer 1975, pp. 495–496; Darwin 1874, pp. 452–453; Wallace 1871, pp. 249–263 and 1889, pp. 277–281).

³⁰ Dominique Lestel considers that ethology is mainly realist-Cartesian: "Contemporary ethology emphasizes an approach to the animal which could be characterized as realistic and Cartesian. It combines fundamental description of the world with stipulation of the legitimate ways of studying it. It supposes that there is a world which is separated from the subject, and that we can provide a genuine description of the animal by investigating the causal and mechanical procedures determining animal behaviour. The possibility of observations without observers, and the description of an animal as a machine, therefore fundamentally define this approach" (Lestel 2011, pp. 83–84).

³¹ Cf. *ibid.*, pp. 84, 89.

³² This approach corresponds to bi-constructivism, which is Lestel's alternative to the realist-Cartesian paradigm (*ibid.*, pp. 83–102).

Darwin's Biosemiotics: *The Expression of the Emotions in Man and Animals*

Darwin wanted to include his considerations on expression in *The Descent of Man*. However, due to the large amount of data accumulated by the naturalist, it was published separately in 1872.³³ Therefore, *The Expression* has to be understood in the context of the argument for continuity.³⁴ Darwin's main antagonist is no more Wallace but Charles Bell:

All the authors who have written on Expression, with the exception of Mr. Spencer – the great expounder of the principle of Evolution – appear to have been firmly convinced that species, man of course included, came into existence in their present condition. Sir C. Bell, being thus convinced, maintains that many of our facial muscles are “purely instrumental in expression”; or are “a special provision” for this sole object. But the simple fact that the anthropoid apes possess the same facial muscles as we do, renders it very improbable that these muscles in our case serve exclusively for expression; for no one, I presume, would be inclined to admit that monkeys have been endowed with special muscles solely for exhibiting their grimaces. Distinct uses, independently of expression, can indeed be assigned with much probability for almost all the facial muscles.³⁵

As a reaction to Bell's design theory, Darwin states that the expression of emotions is not adaptive, which places *The Expression* within the domain of the useless.³⁶ Both zoomorphic anthropology and anthropomorphic zoology are at play in the explanation of expressive movements.

Having gathered data on animal and human expressions from a large diversity of sources, Darwin is able to give three main principles that, combined, should explain most expressive movements:

- I. *The principle of serviceable associated Habits*. Certain complex actions are of direct or indirect service under certain states of the mind, in order to relieve or gratify certain sensations, desires, etc.; and whenever the same state of mind is induced, however feebly, there is a tendency through the force of habit and association for the same movements to be performed, though they may not then be of the least use. Some actions ordinarily associated through habit with certain states of the mind may be partially repressed through the will, and in such cases the muscles which are least under the separate control of the will are the most liable still to act, causing movements which we recognise as expressive.

³³Browne 1985, pp. 308–309; Richards 1987, p. 230.

³⁴It is also important to note that the study of expression constitutes an important argument for monogenism, cf. Winter 2009; Desmond and Moore 2009 [2010].

³⁵Darwin 1890, pp. 10–11.

³⁶Although numerous scholars have noted this particularity of *The Expression* (cf., e.g., Browne 1985; Burkhardt 1985; Richards 1987 and more recently Radick 2010), others, such as Michel T. Ghiselin (cf. Ghiselin 1969 [2003]), have completely distorted Darwin's text by introducing natural selection within *The Expression*. Only four occurrences of natural selection appear in *The Expression* and none of them considers natural selection as an essential explanation of expressive movements (Darwin 1890, pp. 44, 110, 113, 381).

In certain other cases the checking of one habitual movement requires other slight movements; and these are likewise expressive.

- II. *The principle of Antithesis.* Certain states of the mind lead to certain habitual actions, which are of service, as under our first principle. Now when a directly opposite state of mind is induced, there is a strong and involuntary tendency to the performance of movements of a directly opposite nature, though these are of no use; and such movements are in some cases highly expressive.
- III. *The principle of actions due to the constitution of the Nervous System, independently from the first of the Will, and independently to a certain extent of Habit.* When the sensorium is strongly excited, nerve-force is generated in excess, and is transmitted in certain definite directions, depending on the connection of the nerve-cells, and partly on habit: or the supply of nerve-force may, as it appears, be interrupted. Effects are thus produced which we recognise as expressive. This third principle may, for the sake of brevity, be called that of the direct action of the nervous system.³⁷

The principle of serviceable associated habits is certainly the most complex and the most important. Indeed, it presupposes the Darwinian concepts of habit and instinct. In order to explain this first principle, therefore, it is necessary to address its physiological side, its psychological side and the relations between habits and reflex actions. The physiology of the first principle allows Darwin to explain the potential transmission of expressive actions, which is necessary to understand their innate character. Using Max Müller and Herbert Spencer's neo-Lamarckian physiological theory, Darwin states that habits can alter the nervous system by repetition.³⁸ Under the same emotion, nerve-force follows such modified nervous channel, which leads to an instinctive expressive movement. The link between the first and the third principle is evident when the physiology of associated habits is considered.

The psychological side of the first principle is based on the principle of association. An emotion leads to the unconscious accomplishment of a certain action or a chain of actions that can be highly complex. Despite their very different origins, such actions, which are at first conscious and intelligent, are no more distinguishable from instinct, i.e. from the selection of spontaneous variations.

The difference between habit and instinct is central in the consideration of reflex actions. Such actions are "due to excitement of a peripheral nerve, which transmits its influence to certain nerve-cells, and these in their turn excite certain muscles or glands into action".³⁹ Unlike instincts that are centred in the brain,⁴⁰ reflex actions are localised in an affected area of the nervous system. Moreover, reflex actions are mostly not the product of natural selection and are generally issued from habits,

³⁷ *Ibid.*, pp. 29–30.

³⁸ *Ibid.*, pp. 9–13, 30, 41–43, 49–50, 71–75, 80, 209, 358–364.

³⁹ *Ibid.*, p. 36.

⁴⁰ Or in the centre of the nervous system.

which are at first conscious and voluntary.⁴¹ Darwin's double argumentation against Bell and an adaptive explanation of the expression appears. Indeed, the animal accomplishes complex actions, that are at first voluntary and that allow him to obtain satisfaction. Repeated by association, these actions alter the nervous system of the animal, which can then be transmitted to its offspring through the heredity of habits. It is particularly important to underline that the useful actions leading to habits and reflex actions are not selected but correspond to an intelligent reaction⁴² of the animal, taking into account both its structure and the surrounding conditions. Therefore, Darwin disavows the adaptive perspective with respect to the origin and development of the expression of the emotions. Moreover, once the emotion and its corresponding action are associated, which constitutes the expressive character of such movements, the utility criterion becomes superfluous. In sum, the first principle contains Darwin's argument of continuity leading to the consideration of the expression of the emotions as a part of the domain of the useless.

At first sight, the mechanism explaining the principle of antithesis seems trivial. According to the first principle, useful actions are associated to a mental state and become automatic. Such actions correspond to expressive movements. An opposed emotion logically leads to equally opposed movements. However, important implications of the principle of antithesis have to be addressed. Indeed, the limits of convention in the context of expression appear with this second principle of expression. The expressive actions triggered by the principle of antithesis are useless. Movements contrary to other movements initially issued from the first principle cannot be useful, except with respect to communication.⁴³ Although Darwin doubts of the possibility of the voluntary development, by animals, of such complicated movements in order to communicate,⁴⁴ the naturalist recognises that the will can replace simple muscular expressive movements.⁴⁵ With the second principle explaining the expression of the emotions, a possibility of negotiation through communication emerges for the animal.

The name given to the third principle explaining the expression of the emotions seems to isolate it from the two previous principles. Indeed, only the nervous system, independently of the will and habits is considered. In other words, the third principle seems to account for pure useless characters within the domain of the useless. Indeed, the actions explainable by the third principles are not, at first, useful actions as it is the case in the first principle. Moreover, no voluntary action seems to be interfering in the context of the third principle since it concerns parts of the nervous system inaccessible to the will. However, the link with the two other principles

⁴¹ Darwin 1890, pp. 41–44.

⁴² Contrarily to instinctive actions, intelligent actions are issued from conscious choices (from the animal).

⁴³ For example, the position that the cat adopts in order to attack its prey is useful. On the contrary, the movement of the loving cat, opposed to the position of the attacking cat, is of no use. Still, the cat can, by this position, show that it is not going to attack.

⁴⁴ Darwin 1890, pp. 67–68.

⁴⁵ *Ibid.*

of the expression of the emotions is not completely eliminated. All the principles can interact with each other during expressive movements and have Müller and Spencer's neo-Lamarckian physiological theory as common ground.⁴⁶

Certain essential characters of Darwin's theory of expressive signs appear from this (too) brief exposition of the three principles of the expression of the emotions. Reflecting the double argumentation of Darwinian ethology (zoomorphic anthropology and anthropomorphic zoology), expressive movements are issued from an encounter between purely physiological mechanisms and intelligent reactions to structure and surrounding conditions. Moreover, expressive signs are not adaptive and must be studied in the context of the domain of the useless, as it is proved by the extensive use of the heredity of habits, which links all three principles of the expression of the emotions. Finally, the possibility to act on one's expressive movements opens a space in which the animal can negotiate. Thanks to such actions, the animal can wilfully communicate and try to convince its interlocutor. For example, the seductive antics of the males during courtship are entirely based on such actions on expressive movements. Since Darwin thinks that sexual selection is the context of the emergence of language,⁴⁷ allowing one to seduce, convince, praise and blame, and that moral societies are in part built on such exercise of communicative power,⁴⁸ the minimal convention observable in the control of expressive movements appears as a key phenomenon in evolution.

A Saussurean Definition of Ethology and Biosemiotics

The studies trying to conciliate Charles Darwin and Ferdinand de Saussure are few, despite several fruitful possibilities. For instance, it is possible to make an analogy between the Saussurean dichotomy diachrony/synchrony and Darwin's successive considerations of variations and natural selection.⁴⁹ Closer to the perspective of this article, Darwin and Saussure's theories can be compared both historically and theoretically. For example, Winter states that Darwin's theory of expressive signs respects the Saussurean definition of the arbitrariness of the linguistic sign since there is "no semantic relation"⁵⁰ between the expressive movements and the emotion. In sum, an exhaustive comparative work linking Darwin's theory with the Saussurean tradition remains to be done.

An agreement between Darwin and Saussure's epistemology can be found. In the first conference given by Saussure in 1891 for his return to the University of Geneva after years spent in Paris, the linguist defines the science of language as an historical science:

⁴⁶ *Ibid.*, pp. 86–87.

⁴⁷ Darwin 1874, pp. 84, 92 and 1890, pp. 88–100.

⁴⁸ Darwin 1874, pp. 130–134.

⁴⁹ Variations can be studied independently through time while natural selection represents a differential system (cf. Röllin 1980).

⁵⁰ Winter 2009, p. 145.

À mesure <qu'on> a mieux compris la véritable nature <des faits de> langage, <qui sont si près de nous,> mais d'autant plus difficile à saisir dans leur essence, il est devenu plus évident que la science du langage est une science historique et rien d'autre qu'une science historique. C'est de cette qualité de science historique que se réclamera toute espèce d'études linguistiques pour figurer dans une Faculté des Lettres. Comme c'est particulièrement aussi sur cette idée d'histoire qu'il est insisté dans le titre de ce cours – alors que d'autres dénominations comme *Grammaire comparée* sont plus usitées – je crois devoir essayer de faire le commentaire, nécessairement très abrégé et incomplet, du sens qu'a ce mot *histoire* pour le linguiste. C'est sur ce sujet que j'aurais voulu solliciter votre attention presque sans autre préambule, car il contient tout: plus on étudie la langue, plus on arrive à se pénétrer de ce fait que *tout* dans la langue *est histoire*, c'est-à-dire qu'elle est un objet <d'analyse> historique, et non <d'analyse> abstraite, qu'elle se compose de *faits*, et non de *lois*, que tout ce qui semble *organique* dans le langage est en réalité *contingent* et complètement accidentel.⁵¹

Linguistics is not a natural science, contrarily to what could have been inferred from August Schleicher's *Die Darwinische Theorie und die Sprachwissenschaft* (1863).⁵² The study of language is based on the analysis of different languages that are historical realities influenced by the circumstances of human history.

Both Darwin's ethology and linguistics can be considered as historical, and not natural, sciences. Indeed, animal behaviour is studied through anthropomorphic anecdotes. Therefore, animal behaviour is a collection of historical facts and cannot be reduced to abstract laws, except if the model of the seventh chapter of *The Origin* is used. Each animal possesses its own individual history, influenced by a phylogenetic history (itself composed of the sum of individual histories), and a cultural history.⁵³ With the transmission of selective power to the animal, historical contingency is at its peak. Although the expressive movements seem to be triggered by organic laws, due to their physiological determination, Darwin's biosemiotics has to be considered as a historical science and corresponds to the epistemology that Saussure tried to establish in 1891.⁵⁴ The three principles of the expression of the emotions have something to do with animal voluntary actions.⁵⁵ The expressive movements due to the principle of associated serviceable habits are initially the

⁵¹ Cf. Saussure 1891 [1967–1974, IV, p. 5] and 2002, pp. 148–149.

⁵² Cf. Tort 1980.

⁵³ Behaviour can be considered as cultural when the animal actions are not determined by their biology and their environment. It is necessary to add the importance of meaning for the animal considered as a subject (cf. Lestel 2001, p. 368).

⁵⁴ A common mistake has to be avoided here. Saussure uses *historical* as opposed to *natural*. Linguistics is a historical (and not natural) science. With respect to the later distinction of diachronic and synchronic linguistics, both aspects have to be studied by a historical, i.e. not natural, science. In other words, the definition of linguistics as a historical science must not be reduced to diachronic considerations. It is via this very broad sense of *historical* as opposed to *natural* that Darwin's ethology and linguistics can be linked with Saussure's epistemology of the science of language.

⁵⁵ Historical sciences, according to Saussure, study voluntary actions. However, the voluntary character of actions can be more or less pregnant. With respect to language, the voluntary character of linguistic acts is reduced to its minimum by Saussure (cf. Saussure 1891 [1967–1974, pp. 5–6] and 2002, p. 150).

result of actions done on purpose by the animal in order to obtain satisfaction. The principle of antithesis is indirectly the result of voluntary actions. The movements due to the principle of the direct action of the nervous system can be voluntarily used by the animals for their communicative value, as the ones issued from the second principle. As any animal action, the emission of signs is influenced by the three histories of the animal. The individual history determines what kind of emotion the animal is led to feel and what kind of expressive movements it is used to display. The phylogenetic history determines the range of possible movements that the animal is capable of. Finally, the cultural history determines the minimal convention intervening in expressive signs. Therefore Darwin's biosemiotics has to be considered as a historical science based on a historical analysis of expressive contingent facts issued, in their origins, from the voluntary actions of animals.

Conclusion

Darwin's theory of behaviour is far more developed than its limited expression in the seventh chapter of *The Origin*. In order to study the full range of Darwin's ethology, it is necessary to concentrate on his manuscripts, on *The Descent of Man* and on *The Expression of the Emotions*. The Darwinian animal appears as a hermeneutical subject that constructs its own world and that behaves accordingly, taking into account both its structure and the surrounding conditions. Moreover, the Darwinian animal is capable of emitting both voluntary and involuntary signs that can be recognised as such by the animal or the observer (human or non-human). Despite an important physiological determination, most of the expressive movements of the animal are due to the automatisisation of voluntary actions through the heredity of habits. Even movements apparently completely determined by the nervous system can be used on purpose by the animal.

Darwin's non-adaptive ethology and theory of expression is compatible with the Saussurean definition of historical science. Ethology is the historical analysis of behavioural, contingent actions of the animals. Such contingent actions constitute the facts on which ethology (defined as a historical science) is founded. Biosemiotics is the historical analysis of expressive contingent facts issued, in their origins, from the voluntary actions⁵⁶ of animals that are studied by ethology. In sum, biosemiotics is a particular aspect of a global non-adaptive ethology maintaining the continuity between non-human animals and human beings by a historicisation of nature.

⁵⁶The voluntary character of actions is one of the "conditions" of historical sciences as defined by Saussure.

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