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Personalities as epigenetic suites of traits

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Chapter 1. Introduction

1.1. PREFACE: WHY STUDY PERSONALITIES IN ANIMALS

Is it possible that every single individual is unique? That no “copy” of each of us is present somewhere else? How and why do we become as we are? How do personalities develop? And once developed, whatever they are, can they be modified across time?

These are the kind of questions this thesis deals with. They are the same that inspired my interests in behavioural biology long before starting to work on this subject. Then, luckily, I had the opportunity to study personality traits in a bird species, the great tit (*Parus major*), within a much larger programme united in a multilevel system approach encompassing the relations between genes, behaviour, development and evolution in an ecological context. An ambitious matter, no doubt.

I am not the first, nor will I be the last, trying to address such questions. An *excursus*—largely inspired by a paper and a talk of Hans-Peter Lipp of the University of Zürich (1995)—through the historical roots of the subject, leads to the Austrian physician and neuroanatomist Franz Josef Gall (1758-1828), who postulated a biological origin of interindividual variability against the doctrine of his time, which attributed it to differential education.

“From my early childhood on, I always lived in company of many brothers, sisters, and peers. Everyone had something on his own, be it a peculiar talent, a penchant, or another property making him different from the others. Some of them were particularly talented in matters in which they were never instructed, they carved wood or made excellent drawings, others spent all their time painting, while some of them just played hide and search; there were others searching the woods for bird nests or collected insects, snail shells, butterflies, or even built a little garden ... In this way, each of us maintained its own distinctive character, and I never observed a peer who was a mean and perjurious fellow in one year to become a liable friend for the next year ... I also knew that my brothers, sisters and peers received a rather uniform education, or, predominantly, none at all ... Moreover, I observed among the tame and wild animals, of which I always kept a few around me, a similar variability of behaviour as in humans. A given dog would start hunting almost on his own, while another, from the same species and litter, remained untrainable ..., one dog got lost in the neighbourhood, and another homed from remote areas even in his youth. There was a bird who listened attentively to all tunes played to him and memorised them with ease, while another, from the same nest, never learned anything else but his natural song ... It would seem difficult to attribute all this to missing motivation or differential

education. Thus, I had to conclude that such properties were innate, in human beings as in animals. With that, however, one was led to ask for the foundations of such innateness...”(translation by H. P. Lipp, in Lipp & Wolfer 1995)

Today, we know something more about the epigenetic processes (*i.e.*, the interaction between genetic and non-genetic factors) underlying the emergence of the individual personality (see Bateson & Martin 2001 for an overview). The variations are analysed not any more with the two opposing approaches, that of the “genes” and that of the “environment”, but through a synthesis and integration among them. Genes and environment are both indispensable ingredients for shaping individuality. The individual has the inherent ability to follow different developmental trajectories, depending on the environmental conditions to which it has been exposed, by accident or not. The entire life of an individual is characterised by the continuous action of the genes and the environment, never acting independently from each other.

The questions I address here will not be fully or definitely answered by my experiments, carried out exclusively in captive birds reared and living in standard conditions. It is clear that many necessary experiments can not be done in the wild and that nature can not be brought into the laboratory. The compromise is to create semi-natural settings and situations simulating tasks and challenges that animals do encounter in the wild, to use animals originating from wild populations, and to keep a close collaboration with colleagues working on related issues in the field. That is what this project attempted to do. I did not succeed in manipulating physiological factors, such as maternal hormones, or in carrying out cross-fostering experiments, because the breeding performance of the birds in captivity turned out to be often insufficient for achieving a reliable sample size for such experiments (see Chapter 10). In the bird species I used one poor breeding season is one year lost for ontogenetic experiments. In 2000 I had the fortune to have a “good” year, which allowed me to carry out an important manipulation of early food provisioning. I have also not focussed on the possible brain mechanisms and processes related to personality traits and their plasticity, for which we currently can only generate hypotheses. This contribution is a piece of work where I just got closer to the questions, touching upon and manipulating some potentially important factors. The conclusions and the hypotheses generated by my work will be outlined in the general discussion, at the end of the book. Surely, the questions I have faced will continue to tease theorists, biologists, psychologists, philosophers, parents, grandparents and indeed probably most of the human kind.

1.2. CONSISTENT INDIVIDUAL DIFFERENCES

A general aim of ethology is to explain behavioural individuality, which may vary with sex, ecological context, individual history, etc. When taking all these factors into account, still considerable interindividual variation remains. This is true even for standard test situations. It may seem trivial that any biological character varies between individuals. As Slater (1981) pointed out, the average animal emerging after a statistical treatment may possess a set of features that are not possessed by any single individual in the group. However, much of this variation is not random. Within vertebrates and even invertebrates, individuals differ most along an axis from “shy” to “bold” (Wilson *et al.* 1994) or “pro-active”-“reactive” (Koolhaas *et al.* 1999). Actually, this may represent the animal equivalent of the “extrovert”-“introvert” axis in humans (Eysenck 1982; see also Kagan *et al.* 1988 for empirical evidence in children). The “big five” or Five-Factor Model (openness to experience, conscientiousness, extraversion, agreeableness and neuroticism, John 1990) is another popular attempt to categorise correlated personality traits in humans.

In animals “bold” individuals tend to be consistently more aggressive in comparison with “shy” ones; quicker to explore and hence, less neophobic; less socially bound and more prone to disperse; more prone to form routines; less prone to innovate, etc. These contingent behavioural dispositions are assumed to be relatively stable over lifetime in order to qualify them as personality attributes. This phylogenetically widespread and similar differentiation in individual behavioural phenotype may be an unavoidable by-product of nervous system ontogeny, secondarily put in use in a variety of selective contexts in different species. For example, steroid hormones are known to modulate personality traits early in ontogeny, which is used by bird mothers in a variety of species to manipulate their offspring (Schwabl 1993). Individual behavioural phenotype will inevitably be contingent with survival, mate choice, the positioning of individuals in social webs and any kind of decision making. The interpretation of differences at the finest scale between individuals within populations is still unresolved (Wilson 1998), while it will be a major challenge to elucidate the evolutionary effects and functions of interindividual differences. Apart from these basic questions, the field has great potentials for developing basic behavioural theory and is relevant to the applied side, such as commercial farming, animal welfare and conservation biology.

At the start of this project the terminology used in my working environment referring to behavioural strategies that are consistent across time and situations



Fig. 1. Captive adult great tit approaching a novel object.

favoured the term “coping style”. Later, with the hope to capture a broader scientific audience, it was decided to introduce the term “personality”. For this reason, throughout the thesis I shall use both terminologies interchangeably.

1.3. COPING STYLES OR PERSONALITIES

The ability to cope (i.e. to deal successfully) with the enormous variation in environmental conditions, both social and non-social, both temporal and spatial, is a major determinant of the individual ability to survive and reproduce. Within a species interindividual variation in coping strategies exists to deal with these environmental challenges. At the extremes, two apparently opposite styles or sets of personality traits can be recognised: one that is inclined to quick decisions and to actively “manipulate the situation”; and one that is more sensitive to external stimuli, but tries to adjust to the situation in an apparently more passive way. In this thesis I shall often refer to them as the “proactive” and “reactive” styles respectively, a terminology adopted first by J. M. Koolhaas

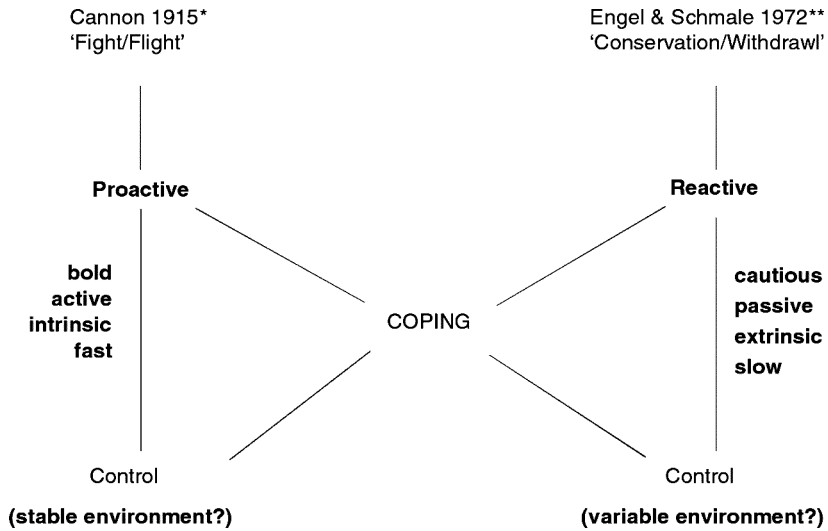


Table 1. Proactive and reactive coping styles.

(University of Groningen), describing the features of aggressive and non aggressive mice, replacing the less specific but more popular terms “active” and “passive” (Koolhaas *et al.* 1999, Table 1). These styles are expressed in different behavioural domains and situations (such as aggression, exploration, foraging), as well as in physiology (HPA reactivity, production of gonadal hormones). The styles have been described or suggested for several species, such as mice, rats, pigs, fishes, tree shrews, farm minks, great tits, man (Koolhaas *et al.* 2001; Broom 2001). By concentrating on the extreme phenotypes through the use of selected lines of animals, one goal of this thesis is to provide a detailed characterisation of personalities in an avian species.

The relative contribution of genetic and non-genetic factors in shaping personality traits is of fundamental relevance to biologists and social scientists. Much work has been done unravelling the genetic factors underlying coping styles, while little is known about the strength of the epigenetic sources of variation. Heritability estimates indicate that there is a substantial genetic basis. In some species, selection experiments have firmly established a heritable component without obvious developmental plasticity (Koolhaas *et al.* 1999). Despite the well-known role of perinatal factors influencing behavioural and physiological responses later in life with a plethora of effects, the ontogenetic

studies rarely consider a sufficiently wide spectrum of behavioural characteristics to be conclusive that the effects are exerted on a coherent set of traits. The same holds for the influence of adult experiences. The other goal of this thesis is to investigate the ontogenetic plasticity of personalities.

The coexistence of the styles within the same population suggests that they are both coherent adaptive patterns in response to every-day challenges, with similar pay-offs, maybe each in a different context or habitat, in terms of lifetime reproductive success. The consequences of different strategies in terms of survival and reproduction have hardly been studied under natural conditions, but they are the focus of three parallel projects on the great tit (see section 1.6) and I shall often refer to them throughout the chapters and the general discussion. The maintenance of different strategies within the same population may be explained by either habitat- or frequency-dependent selection. In the first case, different habitats favour different strategies. In the second case the pay-offs depend on what others in the population are doing: if most individuals are following one strategy, an alternative strategy may bring an advantage and eventually a stable balance in occurrence between the strategies may be reached. Overt behaviour of the organisms themselves may play an active evolutionary role, for example if mate choice or dispersal is related to personality traits, or if shifts in strategies occur during the life of an individual, because these have the potential to affect the genetic variance of the population. In a population of wild house mice the relative frequency of both styles changed in the different phases of dynamic population cycles. This suggests that differential selection on the styles may occur between different phases of the population cycle and that this may even be influential in dynamics of mouse populations (van Oortmerssen & Busser 1989).

1.4. HERITABILITY AND DEVELOPMENTAL PLASTICITY OF COPING

The evidence of a genetic influence of genes on behaviour is clear, although in view of the complexity of the behavioural expression is very unlikely that a simple genetic system is able to control it, and no evidence of particular alleles involved is present so far. Selective breeding for a wide range of behaviours has shown that marked differences between the selection lines appear already after two or three generations, while stable differences are evident after 10-20 generations (Lipp & Wolfer 1995). Examples abound both in mammals and birds, involving for example nest building, aggression, open field behaviour, locomotor activity, avoidance learning, spatial learning in rats and mice; fearful behaviour in farm

minks; mating behaviour, colour preference, timidity in quails (e.g. Bignami 1965, reviews in Benus *et al.* 1991, Lipp & Wolfer 1995, Koolhaas *et al.* 1999).

Heritability is a measure that attempts to quantify the relative importance of genes and environment on a given characteristic. The higher the figure, which can vary between 0 and 1.0, the greater the contribution of genetic variation to individual variation in that characteristic. In humans, twin and adoption studies of personality measures, such as sociability/shyness, emotionality and activity level, have typically produced heritabilities in the range 0.2 to 0.5 (Bateson & Martin 2001). In the great tit birds with a fast speed of exploration differ from birds with a slow speed of exploration in early exploratory behaviour and a selection experiment has produced a realised heritability of 0.54 (Drent *et al.* 2003). The term realised means that the estimate is based on actual genetic improvement resulting from selection.

Although attractive, this measure has some conceptual problems (Bateson & Martin 2001). It is not a quantity that can be defined and/or measured in an unequivocal way. Moreover, it says nothing about the degree in which genes and environment contribute to the processes of development. If a population of individuals is sampled and the results show that one behaviour pattern has a higher heritability than another, it does not mean that genes play a more important role in the development of behaviour with the higher heritability. It could be that the two behaviour patterns have developed in different ways. Environmental influences might have been relatively constant at the stage in development when the more heritable behaviour pattern would have been most strongly affected by experience. The same reasoning holds for groups of individuals differing in their behavioural phenotype. So, the heritability estimate is context- dependent. Another limitation is the wrong assumption that the genetic and environmental variances are independent from each other and can be added together to obtain the total variation.

In a remarkable study the animals' genetic background and their rearing conditions were both varied (Cooper & Zubek 1958). Rats from two genetically inbred strains were each reared in one of three environments, differing in their richness and complexity. The ability to find their way through a maze was measured later in life. Rats from both genetic strains performed equally poorly in the maze if they had been reared in a poor environment and equally well if they had been reared in a rich environment filled with toys and objects. The environmental factor was the only one that mattered. Only in the third type of environment, where the rearing conditions were intermediate in complexity, rats from the two strains differed markedly in their ability to navigate the maze.

Thus, the genetic differences came to expression only in the intermediate environment. An overall estimate of heritability has little meaning in a case such as this, because the effects of the genes and the environment do not add together. They depend on the environment in which they are expressed, while the effects of a particular type of environment depend on the individual's genes. Therefore, experimental studies are necessary in which gene-environment interactions are evaluated, to avoid the risk of misinterpretations of the heritability estimates.

Genes seem to explain about half of the variation in personality traits in great tits housed in standard conditions, while field studies of heritabilities give lower values (Dingemanse *et al.* 2002). Where does the rest of the variation come from? Is it random variation, with little room for evolution? Are there individuals more “plastic” or more prone to change than others? And, could plasticity itself be a trait responding to selection?

The plasticity of behaviour consists in the ability to develop an array of behavioural responses to varying environmental conditions. It involves immediate and often reversible adaptive responses to environmental cues. The range of behavioural responses will increase with environmental variability and the degree of plasticity is under evolutionary pressure (Stearns 1989; Komers 1997). Plasticity is present throughout behavioural development, the process of growth and change from conception to death. Organisms are especially sensitive to change early in life, when there is still active neural proliferation, migration and ongoing maturation of many neurotransmitter systems and synaptic connections in the CNS. At weaning and adolescence changes may be abrupt, and adults may retain the capacity for change of even their most stable characteristics in later life. The probability of change in adulthood is especially prominent following exposure to stressful or emotional conditions at the same time as the individual is exposed to a new experience. Stress enables the individual's behaviour to change, but may also reduce the capacity to change. Cognitive processes, neurotransmitters and hormones are the interpreters of environmental variation to produce a range of phenotypes from the same genotype.

High behavioural plasticity improves the chance of establishing and occupying social niches facilitating reproduction and survival. More subtly, plasticity makes an individual less exposed to the direct pressure of natural selection, driving an individual somewhat less solely dependent on his genes. It makes the organism play an active role in evolution, allowing changes that otherwise might have been prevented by the death of the animal. Plasticity allows

the individual to adjust to new conditions that may reveal heritable variation that was previously unexpressed and opens possibilities for evolutionary changes that otherwise would not occur (Bateson 1988).

At the start of this study there were indications that in great tits plasticity can affect the development of the behavioural differences in the population (Verbeek 1998). In a year characterised by poor environmental conditions (wet and cold spring)—reflected in a weight lower than normal at an age of 8-12 days and frequent starvation episodes—there were about three times more fast than slow birds in the population. This ratio was significantly different from the circa 1.0 ratio observed in “normal” years. It was hypothesised that either fast nestlings survived better in adverse situations, or that retardation of growth and enhanced sibling competition in the nestling phase stimulated the development of a fast phenotype.

The plasticity in the development of personalities may be further subject of maternal influences, shifting the mean phenotypic value of the offspring in the next generation. The discovery in the early 90s that the female transmits androgens to her eggs exerting pronounced influences on offspring development (Schwabl 1993) translated to birds what was already known from decades in mammals about pre-natal influences of gonadal hormones. It is conceivable that these hormones influence personalities, since it has been suggested that perinatal androgens differentiate coping styles in mice (Compaan *et al.* 1992). This is of interest, since cross fostering of eggs, a common procedure to rule out maternal effects in selection experiments with birds and also used in great tits (Drent *et al.* 2003), would not account for effects of yolk compounds in the eggs.

1.5. STRESS AND COPING

The concepts of personalities and coping styles are tightly linked to the concept of stress. The stress response, in spite of being studied mostly by physiologists, pharmacologists and psychopathologists, is considered to be a highly adaptive piece of physiology when looked by eyes of biologists with an evolutionary approach. The stress response is itself a measure of plasticity.

An animal faces stress when exposed to adverse conditions eliciting responses that attempt to deal with the stressor and help return to a homeostatic condition. It is usually said that when the balance is back to normal the animal has coped with the stress. Animals exposed to a situation where they can not alter their behaviour in response to a stressor will give

responses that lead to chronic stress, with the potential to be abnormal and maladaptive if coping is unsuccessful. Here, I regard stress from a functional point of view in terms of adaptive responses to unpredictable, acute, episodic and short-lasting situations.

Mechanisms have evolved that rapidly trigger changes to cope with such stressful events. Basically, two main systems are involved, complementing each other as an emergency system.

- (i) The sympathetic-adrenal-medullary system is involved in the quasi-instantaneous (seconds) activation of physiological factors such as a rise in the release of catecholamines, which induces an increase in heart rate and blood pressure, glucose and free fatty acids necessary for an immediate increase in muscular activity to escape or fight the source of stress. A rise in core body temperature, detectable after minutes, is also mediated via this system.
- (ii) The hypothalamus-pituitary-adrenal axis is slower (minutes). It involves the rise in the release of the adrenal hormone corticosterone, which has a cascade of multiple effects, among which the mobilisation of energy reserves (by enhanced gluconeogenesis), induction of escape/dispersal behaviour, increase in activity/foraging.

During my work I have tried to activate both “emergency systems” in relation to personality in great tits, using different kind of stress sources. The link with personalities is crucial, since so far a large inter-individual variation has been observed in the stress response in birds (especially adrenocortical response): apart from gender, age and seasonal differences, some individuals only show a weak stress response, whereas other individuals in the same population show rapid and conspicuous responses. In birds the bases for such variations and their ecological consequences are unclear (Schwabl 1995; Silverin 1998). By looking at the stress response in relation to personality types, we have built a solid framework to interpret and explain them.

In one experiment I tried to replicate the findings in mice, but now in great tits, that animals with a reactive style have a higher HPA reactivity to stress (Koolhaas *et al.* 1999). In another one, I tried to quantify the observation by Verbeek *et al.* (1999) that the fast explorers (proactive style) take more time than slow explorers to initiate a new interaction after losing a male-male contest. In both experiments and in a third one I also used body temperature and breath rate as physiological markers of the stress response.

1.6. THE GREAT TIT

My animal model is the great tit (*Parus major*), a small, highly territorial, non-migratory passerine bird and a key species for field studies (Fig. 1). It was chosen for the following reasons: (i) its behavioural ecology is well known in many respects; (ii) variation in behaviour exists which seems to fall within the types of coping (iii) it can be kept in captivity, allowing investigations under laboratory-controlled conditions.

As a follow-up of the finding of consistent individual differences in great tits' early exploratory behaviour and aggression, two genetically selected lines for the former trait have been established (Verbeek *et al.* 1998; Drent *et al.* 2003). The selection was based on a composite trait assessed in the juvenile phase, shortly after fledging: the speed of exploration in an unfamiliar environment and the speed of approach to a novel object. This selection resulted in clear evidence for the genetic basis for these traits, since the scores rapidly diverged between the two lines already after two generations (Drent *et al.* 2003, Fig. 2). The two "types" of individuals have been labelled "fast" and "slow" explorers (henceforth I indicate the two lines as SLOW and FAST with capital letters) and they have been hypothesised to reflect the proactive and reactive strategies of rodents, since they differ in traits like exploration, aggression and routine formation similar to the mice model. Virtually, all studies on coping styles have been done with domesticated animals or laboratory rodents, often from a stress physiology or an animal welfare perspective. These lines created the unique possibility to study in a wild species how genetic make-up and environmental factors interact during development to determine an important phenotypic trait that may profoundly determine individual fitness and exert effects at the population level.

In 1998 three research groups in The Netherlands, at the NIOO, (Dr. P. J. Drent, Prof. Dr. A. J. van Noordwijk), the UU (Prof. Dr. G. De Jong), and the RUG (Dr. T. G. G. Groothuis, Dr. J. M. Tinbergen, Prof. Dr. J. M. Koolhaas) teamed up under coordination of T. G. G. Groothuis with the following goals: to quantify the natural variation of the trait in the field both in juveniles and adults and estimate fitness consequences in different spatial and temporal conditions (N. Dingemans, Dr. C. Both); to analyse the genetic structure of inheritance (K. van Oers); to characterise the nature of the differences and the influence of environmental factors on their development (C. Carere). The unifying framework was the question of the origin and persistence of phenotypic variation in behavioural traits within populations.

The project forming the basis for this thesis deals specifically with the characterisation, developmental and plasticity issues.

1.7. QUESTIONS

By using animals resulting from a directional selection for juvenile exploratory behaviour I had two main goals: 1) to provide further evidence that the concept of coping styles or personalities holds for great tits as well; hence, I characterised the nature of the line differences in more detail; 2) to study the degree and the possible way of action of ontogenetic plasticity in shaping heritable styles; hence I manipulated rearing condition.

I characterised personalities in great tits belonging to the two selection lines (3rd to 6th generation, except for one experiment in which birds were sampled from a wild population and only phenotypically characterised) by searching for line differences in an array of situations. I was interested whether indeed they generalise to a number of situations and contexts across the lifespan. The one where I put most emphasis on is the stress response, because through this I could infer possible physiological mechanisms underlying the strategies. In one experiment I challenged the experimental subjects of the two “types” inducing a social conflict following a territorial intrusion. In another experiment I induced a situation thought to simulate a predation attempt by using a “capture and handling protocol” of the experimental subjects (Silverin 1998).

I looked at ontogenetic plasticity with both a descriptive and an experimental approach. First, I explored when during ontogeny the differences emerge, including levels of yolk maternal hormones, and if they are stable and persist in adulthood. Next, I experimentally created situations expected to induce plasticity by rearing the animals under different conditions during early life. I checked whether the induced plasticity affected the set of characteristics that make up a personality and whether the results of plasticity are transient or produce stable patterns.

1.8. STRUCTURE OF THE THESIS

The thesis is organised into three topical sections. Section A (Chapters 2 and 3) depicts the behavioural features of the two lines of great tits in an array of situations and tests the domain generality of the trait. The data presented in Chapter 2 are the result of a long-term longitudinal study and provide also an indication of plasticity across age. Section B explores how adult individuals

entailing those features depicted in the first section cope with stress of social (Chapters 4 and 5) and non-social (Chapter 6) origin. Section C looks specifically towards ontogenetic plasticity, both descriptively, exploring how early and under which circumstances the features are emerging (Chapters 7 and 9), and experimentally, questioning to which extent and for how long they are able to change upon ontogenetic perturbations (Chapter 8). Chapter 10 tries to summarise and discuss all the findings in a coherent framework.

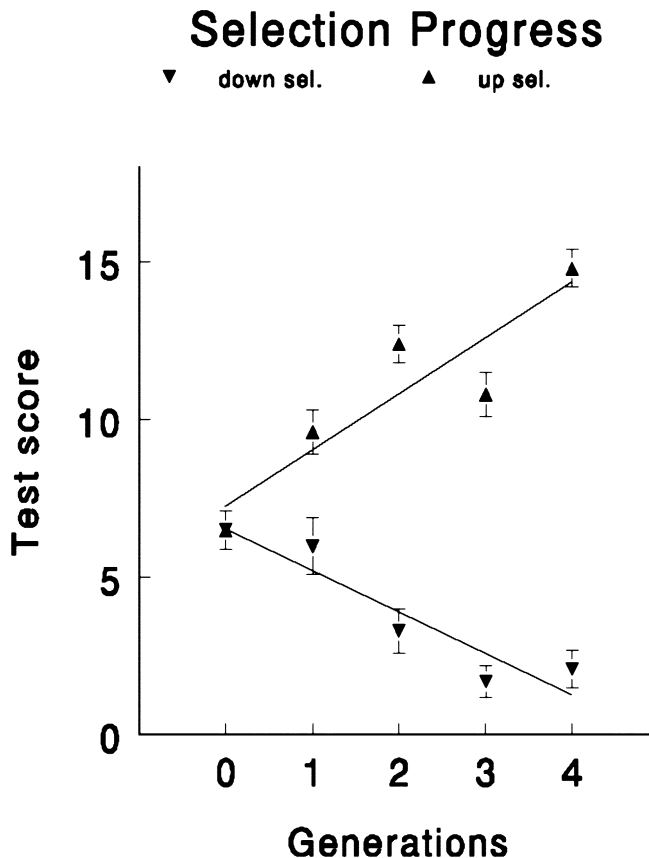


Fig. 2. Response to artificial selection per generation. Mean values (\pm SEM) for a combined score in two behavioural tests performed at 35 days after hatching: exploring an unfamiliar environment and a novel object in a familiar environment. Both the selection for FAST (up) and SLOW (down) exploration speed were started from a common base population (generation 0) collected in the field (Drent *et al.* 2003).

