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DNA fingerprinting analysis of rabbits from lines divergently selected for high and low open-field activity*

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The aim of the study was to analyse whether a successful divergent selection for open-field activity (OFA) in rabbits has resulted in differences in DNA fingerprinting pattern and genetic parametres of diversity. We also scanned DNA fingerprinting profiles for searching minisatellite alleles potentially linked to genes determining the trait under selection. Rabbits derived from the 8th generation of the lines selected for high (H) or low (L) locomotor OFA were profiled for DNA fingerprinting using *Hinf*I enzyme and 33.6 *multilocus* probe. The H and L lines represent different, *i.e.* active and passive coping strategies in a novel situation.

Selection for H or L locomotor OFA did not affect significantly the molecular parametres of genetic diversity. However, the analysis of band patterns for individual and pooled DNA fingerprints revealed a specific band for the L line at 15 kbp. No specific bands for the H line were detected. The results presented provide evidence of a possible linkage between minisatellites and OFA in rabbits and demonstrate that studies on the H and L lines may give rise to a new strategy in animal breeding and selection for traits related to animal welfare (locomotion and fear-related emotional behavior) and to the study of genetic background of hyperactivity disorders, e.g. ADHD.

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The open-field activity (OFA) test originally described by Hall [1934] is one of the oldest behavioural tests for studying animals' emotionality aroused by exposure to a new environment The procedure consists of subjecting an animal, usually a rodent, to an unknown environment from which escape is prevented by surrounding walls [Walsh and Cummins 1975]. The OFA test has become very popular and its use extended on calves, pigs, lambs, rabbits, pullets, primates, honeybees and lobsters. Current opinion about OFA test holds that it is useful for complex individual behavioural strategies in which general arousal and exploratory activities compete with fear-related behavioural inhibition [Boissy 1995, De Passille *et al.* 1995, Stam *et al.* 1997, Prut and Belzung 2003, Carola *et al.* 2002, Mignon-Grasteau *et al.* 2003].

Behaviour of rodents in the open-field depends mainly on the tactile sensory factors. It should also be noted that exploration can be increased by some factors such as food or water deprivation: it is therefore very important to verify that a given treatment does not act on such variables, before concluding about possible effects on anxiety-like behaviours. Finally, open-field behaviour also depends on lighting conditions and the light-dark cycle, so that it may be relevant to ensure that a treatment does not modify internal clock-related behaviours and to test the treatment under different lighting conditions. Underscoring problems with interpretation of the results is a fact that the OFA test has been used for very different purposes, e.g. to assess strain differences in exploratory behaviour in rats [Schmitt and Hiemke 1998] and rabbits [Zelnik *et al.* 1990], to evaluate crossbreeding effects and individual heterosis in rabbits [Rafay and Fl'ak 1998] and effects of handling [Denenberg *et al.* 1977, Kersten *et al.* 1989, Hirsjari and Valiako 1995, Schmitt and Hiemke 1998]. However, the majority of investigations using the OFA test were concerned with the behavioural effects of anxiolytic drugs [e.g. Ramos *et al.* 1997, Cools and Gingras 1998, Choleris *et al.* 2001, Mechan *et al.* 2002, Prut and Belzung 2003]. According to Crawley *et al.* [1997] there is no single trait which reflects emotional reactivity or anxiety and thus genes involved in the OFA may simultaneously be involved both in locomotion and exploratory activity and in fear, anxiety or other emotional traits.

The divergent selection for behavioural traits has often been applied to obtain strains which can be used to test hypothesis about genetic background of these traits [e.g. Turri *et al.* 1999, 2001, Flint 2003]. Significant linkages to responses to a novel environment stress were found for ACTH gene and for genes determining glucose level. On the other hand, for behavioural reactivity traits (locomotion, vocalizations, defecations, explorations) gene effects of low amplitudes only were found [Desautes *et al.* 2002].

In comparison with microsatellites, the studies on the OFA using minisatellite analysis are generally absent and we are aware of only one paper describing the use of DNA fingerprinting (DFP) method in rabbits [Sudo *et al.* 1993]. Here we applied DFP method to rabbit lines selected for high (H) or low (L) locomotor activity score in the

OFA test. The present study is the first, to our knowledge, in which rabbit genotypes were scanned by DFP method using human minisatellite probe 33.6 and also the first with respect to the OFA in selected lines of rabbits.

The DFP produced with *multilocus* probes detecting several types of repeats provide a useful tool to assess the genome as a whole [Russel *et al.* 1993]. Particularly, in the absence of detailed knowledge of the composition and architecture of the genes involved, *multilocus* probes may provide an interim technique for assessment of the genome, until more detailed knowledge is obtained. As a useful tool for the assessment of genetic distances between genetic groups as well as for accurate estimation of inbreeding we used DFP technique to compare H and L lines and for assessing genetic diversity within them. Moreover, we used DFP technique as an efficient method for genotyping existing markers. These markers should substantially accelerate the mapping of genes affecting selected trait [Schlötterer 2004].

In the earlier experiment two lines of rabbits were divergently selected for high (H) or low (L) open field activity (OFA) over eight generations [Daniewski and Jezierski 2003]. The selection response was most evident up to the 3rd and 4rd generation, in H and L line, respectively. This fact may argue that the OFA is heritable and determined oligogenically by only few genes. Indeed, the realized OFA heritabilities in the first three generations were 0.46 and 0.23 for H and L line, respectively. However, during the next four generations, a decrease of the selected trait was observed in the H line to the level recorded at the start of selection, whereas in L line the selected trait and its variability reached values close to zero. The aim of the present study was to screen, using molecular methods, the genomes of rabbits from the two obtained lines differing in the selected behavioural trait.

Material and methods

Animals

The rabbits derived from the eight generation of the lines selected divergently for high (H) or low (L) open-field activity (OFA) at the Institute of Genetics and Animal Breeding, Jastrzębiec. The foundation population for the selection experiment (60 males and 60 females) derived from the Institute's own New Zealand White outbred rabbit stock. A detailed description of the housing and feeding as well as of the selection procedure was given by Daniewski and Jezierski [2003].

Fourteen males from the H and fourteen from the L line were chosen randomly for DNA fingerprinting analysis. The equal amounts of DNA from 10 animals of each line were mixed for pooled patterns while four other were chosen for individual patterns.

The experimental procedure and housing/feeding of rabbits were both approved by the Third Local Ethics Commission on Animal Experimentation.

DNA fingerprinting

For assessing genetic parametres within and between lines two types of DNA fingerprints were prepared: in one case individual DNA samples (four individuals per line) and in the other case DNA mixes using equal amounts of DNA from 10 animals within lines. DNA fingerprints of individual DNA samples were used to determine the band sharing (BS) degree and other genetic parametres within lines. Pooled DNA was used to produce DNA fingerprinting patterns, which are representative of each of the two lines considered.

DNA was isolated with phenol-chloroform extraction from 0.5 ml of ear blood collected under local anaesthesia (lignocainum). DNA was digested overnight (about 16 hours) with *Hinf*I (POLGEN, Poland) enzyme. Similarly, DNA fragments on the gel were transferred to nylon membrane over the same period of time. A filter previously dampened in 1×SSC was placed in glass tube. The filter was pre-hybridized for 40 min at 50°C in a buffer composed of: 0.495 M Na_2HPO_4 (pH 7.2) (AppliChem, Germany) and 0.1% SDS (AppliChem, Germany) – 100 µl of buffer per 1cm^2 of filter. Next, the buffer was changed on hybridization with the same composition as previously, but with an addition of 1% casein, as a blocking factor, and with 8 µl of probe 33.6 (CELLMARK DIAGNOSTIC). The filter was hybridized for 30 minutes at 50°C. The chemiluminescent signal was detected using Lumi-Phos® 530 solution (CELLMARK DIAGNOSTIC) and transferred to Kodak X-ray film.

Computational analysis

The DFP analysis included only bands representing fragments larger than 2 kb. Banding patterns were compared between lines to classify shared and non-shared bands. Bands were regarded as non-shared if they differed in their position more than half of the band width and if the ratio of the intensities was less than 1:2. The band patterns were analysed using visual inspection and the software DNA*ProScan*. The results were derived from two inspecting persons. Correlation between them was found close to 1.

Statistical

Based on the results of patterns generated by DNA fingerprinting mathematical calculations were done to compare analysed individuals and to assess genetic distance between lines. Main statistical parametre of band patterns, *i.e*. band sharing (BS), based on the number of common bands between two individual samples, was used to describe the similarity between profiles of DFP. On the basis of BS parametres the probability of identity – P [Wetton *et al*. 1987], the total number of distinct and recombinationally separable hypervariable *loci* – L [Lynch 1990], average genetic variation between individuals – AVB [Kuhnlein *et al*. 1989], heterozygosity – H [Stephens *et al.* 1992], and genetic distance between lines – DL [Lynch 1990] were determined to compare analysed individuals within and between lines. All means were compared using the General Linear Models procedure [SAS Institute 1990].

Band sharing (BS) was calculated after Jeffreys *et al*. [1985] according to the formula:

where: N_{ab} – number of bands shared;

$$BS = \frac{2N_{ab}}{N_a + N_b} \quad (1)$$

N_a and N_b – total number of bands scored in samples A and B, respectively.

Based on BS, the **probability (P)** that two randomly selected individuals show identical banding patterns was calculated after Wetton *et al*. [1987] according to the formula:

where: bs – mean band sharing (BS);

$$P = (1 - 2bs + 2bs^2)^{N/bs} \quad (2)$$

N – mean number of bands.

On the basis of mean BS and the mean number of bands (N) in individuals of the analysed population the **total number of distinct and recombinationally separable hypervariable *loci*** (L) was computed after Lynch [1990] according to the formula:

where: S_k – frequency of the *k*-th band;

$$L = \sum_{k=1}^{A} (1 - \sqrt{1 - S_k}) \quad (3)$$

A – total number of different bands;

n – number of individual samples.

Genetic variation within lines. The estimation of genetic variation within H and L lines was based on band sharing (BS) and band frequency. Whereas band sharing is the main parametre when evaluating DNA fingerprints, band frequency corresponds to allele frequency, which is the main parametre when dealing with other genetic markers. All values were averaged over all individuals in the examined populations. The values are given as arithmetic means with standard deviations (SD).

Based on band frequency, the additive inverse of mean band frequency called **average genetic variation between individuals** (AVB) was calculated after Kuhnlein *et al.* [1989] according to the formula:

where: v_i – frequency of band *i*;

$$AVB = 1 - \frac{1}{n\left(\sum v_i\right)} \quad (4)$$

n – the number of bands counted.

The second estimator calculated with band frequency was the **heterozygosity** (H), identified after Stephens *et al*. [1992] according to the formula:

where:

S_k – frequency of the *k*-th band;

$$H = \left(\frac{2n}{2n-1}\right) \times \left[\sum_{k=1}^{A} \frac{S_k}{A} - \sum_{k=1}^{A} \left(1 - S_k\right)^{0,5} - 1\right] \qquad (5)$$

A – total number of different bands;

n – number of individual samples.

Coefficients of correlation between the three measures of genetic variation within population: APD, AVB and H were calculated using the correlation procedure.

Genetic distance between lines. Genetic variation between the two lines was also estimated basing on band sharing and band frequency values averaged over all banding patterns obtained. The genetic distance (DL) between lines was computed by adaptation of the BS levels between lines for relatively unbiased estimates of genetic distance after Lynch [1990] according to the formula:

where:

S_{ij} – average band sharing between line *i* and *j*;

S_i and S_j – mean BS between individuals within lines [Lynch 1990].

$$DL = -\ln\left(\frac{S_{ij}}{\sqrt{S_i S_j}}\right) \qquad (6)$$

Results and discussion

The analysis of band patterns for individual and pooled DNA fingerprints resulted in the identification of one specific band for L line. No bands specific to H line were detected (Photo 1).

To explain whether the OFAs are determined only by particular genes, or by differences in genetic variation, measurements of these parametres were made. The major part of genetic variation was generated by the bands representing minisatellites of high molecular weight. This was determined by a higher probability of differences in the length of minisatellites represented by these bands. Analysis of DFP showed high variation within and between lines (Tab. 1 and 2).

The genetic variation within H line was not found significantly different from that within line L. It is a classical phenomenon, observed both in animals and humans, that differences in only subtle traits do not affect the overall inter-group differences.

The divergent selection for high and low locomotor OFA in rabbits did not signifi-

cantly affect the genetic parametres of molecular diversity. However, a specific band for the L line at 15 kbp and no specific bands for the H line were detected.

One of the main questions concerns the mechanism by which in H line the realized

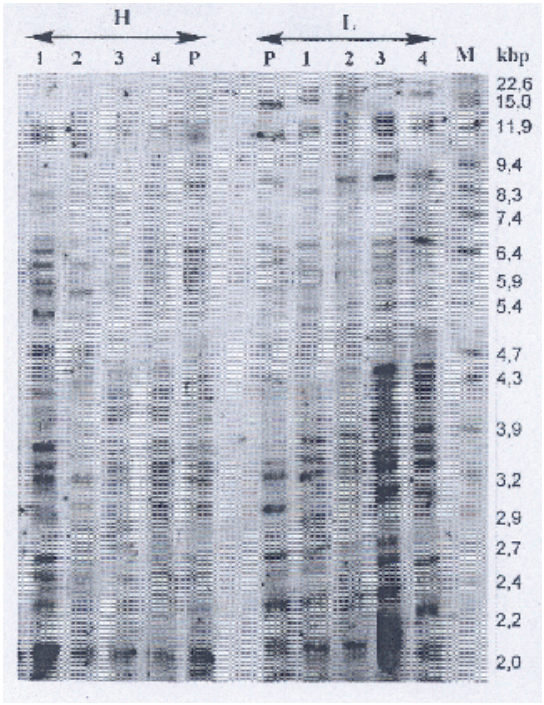

Photo 1. DNA fingerprinting patterns of rabbits of H and L line. 1-4 – individual patterns; P – pooled patterns. M – size marker.

Tab le 1. Mean genetic parametres of diversity and their standard deviations (SD) within line H and L

Line	Pro ba	BS		N		L	P	AVB	H
		mean	SD	mean	SD				
H	33.6	0.770	0.070	13.20	1.920	8.940	5.570×10^{-4}	0.370	0.290
L		0.747	0.120	13.80	1.780	8.660	1.310×10^{-4}	0.340	0.280

BS – band sharing.
N – mean number of bands.
L – number of independent loci.
P – probability of identity patterns.
AVB – average variation of bands.
H – heterozygosity.

Table 2. Genetic parametres between lines. DL – genetic distance by Lynch [1990]

Parametre	Line	
	H	L
Band sharing	0.714	
Genetic distance	0.060	
Specific bands	0	1

heritability decreased during selection (Fig. 1). The divergent selection for high and low locomotor OFA did not change significantly the genetic parametres of diversity. However, this phenomenon suggests the possible epistatic interactions in genome. Flint *et al.* [2003] estimated the interaction effect between any two *loci* to be less than 5% of the total phenotypic variance in mice. However, it is possible that the epistatic part of variance is different between species.

Another question concerns the mechanism by which H line-specific minisatellites cosegregate during selection: is it linked with gene(s) determining the selected trait or do they participate in their expression? Though minisatellites are usually noncoding, some of them may also participate in gene expression. Through the participation of

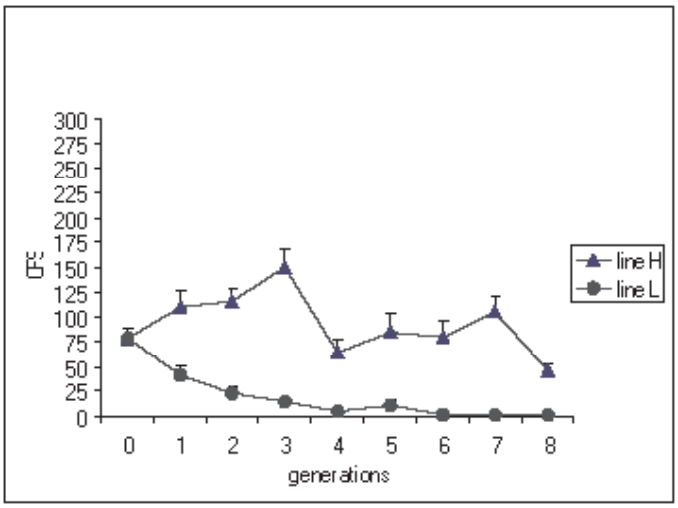

Fig. 1. Mean OFA and their SEM in lines H and L in consecutive generations (Mann-Whitney U test): between lines P<0.0001, between sexes P<0.69 and Kruskal-Wallis test: between generations within lines P=0.0000.

minisatellites in many significant cellular processes (*e.g.* regulation of transcription and translation) as well as in maintaining the stability of mRNA or modification of protein activity, they may be engaged in various physiological dysfunctions or in predestining

to diseases. Minisatellites of pathological lengths are created as a result of mutations of the original, progenitor forms.

The transcription functions of minisatellites may be illustrated by many examples, but in respect to the trait selected in this study (*i.e*. activity) particularly interesting is the minisatellite present in the gene of transporter protein or serotonine which may be involved in proneness to depression or neuroticism [Lesch *et al.* 1996]. Another possible minisatellite is located in the 3'untranslated region (3'UTR) of the dopamine transporter (DAT) and also that present in the D4 dopamine receptor. As those genes are expressed at a high level in the limbic areas of the brain, their products may be associated with cognitive and emotional behaviors and may play a role in many attention deficit hyperactivity and other dopamine-related disorders [Benjamin *et al.* 1996].

The present work provides evidence of a possible linkage between minisatellites and open-field activity in rabbits. The results demonstrate that studies on the H and L lines may give rise to a new strategy in animal breeding and selection for traits related to animal welfare (locomotion and fear-related emotional behaviour) and to the study of genetic background of hyperactivity, e.g. ADHD.

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Analiza DNA fingerprinting linii królików selekcjonowanych rozbieżnie na wysoką i niską aktywność w otwartym polu

S t r e s z c z e n i e

Celem badań było określenie, czy selekcja królików na aktywność w otwartym polu spowodowała zróżnicowanie we wzorze DNA fingerprinting, a także czy efektem tej selekcji jest zmiana genetycznych parametrów zmienności na poziomie molekularnym. Ponadto wzory DNA fingerprinting analizowano pod względem obecności specyficznych alleli minisatelitarnych, które potencjalnie mogą być sprzężone z genami determinującymi selekcjonowaną cechę. Profilowanie DNA fingerprinting przeprowadzono na ósmym pokoleniu królików selekcjonowanych na wysoką (H) i niską (L) aktywność w otwartym polu, z użyciem enzymu *Hinf*I i wielopozycyjnej sondy 33.6. Rozbieżna selekcja nie spowodowała znaczącej zmiany w genetycznych parametrach zmienności. Jednakże analiza indywidualnych i reprezentatywnych wzorów prążkowych pozwoliła na identyfikację w linii L specyficznego allelu minisatelitarnego o długości 15 tysięcy par zasad. Nie wykryto specyficznych alleli u osobników linii H.