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Differences in adaptive abilities of three breeds of Chinese pigs.

Behavioural and neuroendocrine studies

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Summary

In three breeds of Chinese pig (Mei-Shan, Jin-Hua, Jia-Xing) the general behavioural reactivity was investigated, as well as reactivity of the pituitary-adrenal axis and the sympathetic-adrenal medullary system. A F2 cross (Landrace × [Mei-Shan × Landrace]) was used as control. These breeds displayed a large range of behavioural reactivity to a novel environment test, with females generally more active than males. Chinese pigs had higher plasma levels of cortisol and showed a sexual dimorphism in plasma ACTH levels. Complex relationships were found between behavioural reactivity and endocrine characteristics, a high behavioural reactivity being associated with low plasma levels of ACTH, corticosteroids and adrenaline. These results, beside their interest for further understanding of the recently introduced chinese breeds, open new perspectives for further studies of relationships between hormones and adaptive behaviours.

Key words : Pig, Chinese breeds, behaviour, neuroendocrinology.

Résumé

Etude comportementale et neuroendocrinienne de trois races de porcs chinois

La réactivité comportementale et neuroendocrinienne (ACTH, cortisol, catécholamines) de trois races de porcs chinois (Mei-Shan, Jin-Hua, Jia-Xing) a été étudiée dans des tests standardisés. Un backcross (Landrace × [Mei-Shan × Landrace]) a été utilisé comme contrôle. Une large gamme de réactivité a été observée lorsque les animaux sont introduits dans un environnement nouveau, les porcelets de race Mei-Shan étant les moins actifs. Par ailleurs les femelles se sont révélées plus actives que les mâles. Les porcs chinois ont des taux circulants de cortisol, deux fois plus élevés que les animaux croisés et sont plus résistants à la freination de l’axe corticotrope par la dexaméthasone. Les taux d’ACTH sont sans rapport avec les taux de cortisol, mais sont corrélés de façon négative avec la réactivité.
comportementale des animaux et sont plus élevés chez les mâles. La réactivité comportem-
mentale est également corrélée de façon négative avec les taux circulants d'adrénaline et
de cortisol. Au-delà de leur intérêt pour la connaissance des races de porcs chinois récem-
ment introduites en France, ces résultats ouvrent de nouvelles perspectives pour l'étude
des interrelations entre hormones et comportements adaptatifs.

Mots-clés : Porcins, races chinoises, comportement, neuroendocrinologie.

I. Introduction

Differences in the way different breeds adapt to environmental challenge are
taken observed. However, this has not been the subject of much experimental work
in farm animals, except in poultry where several selection experiments have been
donducted either for behavioural traits or for pituitary-adrenal activity (SIEGEL, 1979).

The main difficulty when studying the influence of genetic factors on adaptive
abilities is not to describe interbreeds variations but rather to integrate them in an
adequate conceptual framework. It has been suggested that there are two basic strate-
gies for coping with environmental challenges : active responding, best illustrated by
the fight-flight reaction, and passive responding in the form of freezing, submission
and withdrawal. Both types of responding have different neuroendocrine correlates :
active responding is mainly associated with release of catecholamines by the adrenal
medulla and the activation of the sympathetic nervous system ; passive attitudes are
rather related to the stimulation of the pituitary-adrenal axis (for a discussion of the
evidence in favor of this dichotomy in farm animals see DANTZER et al., 1983 ;
DANTZER & MORMEDE, 1983). In addition there are complex relationships between
hormones and adaptive behaviours, in the sense that hormonal activities by themselves
are able to influence the way the animals react to aversive events while at the same
time the animal's behaviour affects hormonal reactions to environmental stressors. The
outcome of adaptation is the net result of these two combining mechanisms.

The present study was undertaken to further substantiate the importance of breed
differences in adaptive abilities by studying both behavioural and neuroendocrine
responses to psychological stressor of three breeds of Chinese pigs recently introduced
in France. Pigs from a F2 cross with Landrace were used as controls since there
was no pure European breed in the same environmental conditions at the time these
experiments were carried out.

II. Materials and methods

A. Animals

The purebred piglets used in this study were offspring from the Chinese
breeders introduced in France in 1979, either from the first [Jia-Xing (JX), Mei-Shan
(MS) and Jin-Hua (JH) breeds] or the second (JH) generation. Crossbred animals
originated from a backcross (MS × Landrace) × Landrace. Piglets were weaned at
30 days in the maternity pens (1.95 m × 2.5 m) and were kept on straw. They received ad libitum food and were 8-9 weeks old at the time of testing. The experimental animals originated from two litters for each breed (except for the JH breed in which animals were taken from one first-generation and two second-generation litters, due to the reduced size of the available litters). Crossbred males were castrated, purebred males were intact. The main characteristics of these Chinese breeds have already been described (Legault & Caritez, 1982; Rombauts et al., 1982; Legault et al., 1982).

**B. Behavioural tests**

- Exposure to a novel environment. The inside of a lorry (2.4 m × 1.2 m) was used as a test arena. Painted lines separated the floor into 8 sections (0.6 m × 0.6 m). Wood shavings were spread on the floor and replaced between successive animals. Piglets were individually introduced into this novel environment for a 10-min period. Different behavioural activities were recorded by an observer located outside the lorry, together with the time of their occurrence, with the aid of a data collector (Electro General Datamyte 1000): locomotor activity (number of sections entered), vocalizations (squeals and grunts).

- Neophobia test. After the novel environment test, animals were deprived of food for 24 hours. At that time, they were again introduced into the lorry where a cylindrical trough with food had been placed. Latency time for first contact with the trough and for feeding were recorded with a cut-off time of 5 min.

**C. Endocrine measures**

- Blood samples. Blood (5 ml) was taken from the jugular vein of animals restrained on their back in a V-shaped trough. An average time of 30 minutes elapsed between catching the animal out of its pen and the completion of blood sampling. Animals were sampled before the novel environment test, immediately after it and 20 mn later, to measure basal plasma levels of glucocorticoids, ACTH and catecholamines and their response to the psychological stimulus of exposure to the novel environment. In addition, blood was taken from other animals (4 males and 4 females in each breed except for JX) in order to get a more accurate measure of basal glucocorticoid and ACTH levels. Blood was taken between 9:00 a.m. and 1:00 p.m., when a sustained high adrenocortical activity has been described in pigs (Favre & Moatti, 1977).

A dynamic test of hypophyso-adrenocortical function was carried out in 4 male and 4 female MS, JH and crossbred. Dexamethasone (Azium®, Galena lab.) was injected in the evening (7.00 p.m.) by the intramuscular route (20 μg/kg). The next morning (between 8 and 9.00 a.m.) blood was taken and ACTH (Synacthène immédiat®, Ciba, 5 μg/kg) was injected i.m. Another sample was taken one hour later for corticosteroid measurement.

Blood was taken on heparinized tubes for glucocorticoid and catecholamine assays and on EDTA for ACTH assay. Tubes were kept on ice until centrifugation and plasma aliquotes were frozen (— 20 °C) pending analysis for a maximal storage time of 4 months.
— Glucocorticoid and ACTH assays. Plasma glucocorticoid were measured by a protein binding assay (Murphy, 1967) after dichloromethane extraction. Pregnant woman serum was used as the transcortin source, tritiated cortisol as the tracer and dextran-coated charcoal as the adsorbant of the unbound fraction. A commercial kit (C.E.A., Gif-sur-Yvette) was used for ACTH radioimmunoassay. The use of these methods for studies in pigs has been previously validated (Favre & Moatti, 1977; Mormède & Dantzer, 1978 a). An inter-assay variability of 10 p. 100 was typically found and intra-assay variability averaged 7 p. 100.

— Catecholamine assay. Plasma catecholamines were measured by a radioenzymatic assay (da Prada & zurcher, 1976; Sole & Hussain, 1977). Briefly, a tritiated methyl group was transfered from radioactive S-adenosyl-methionine to adrenaline and noradrenaline with semipurified catechol-0-methyl transferase from rat liver. The tritiated methoxyamines were extracted, separated by thin layer chromatography, eluted and oxidized into radioactive vanillin, the radioactivity of which was measured by scintillation spectrometry. Inter-assay variability for plasma samples averaged 20 p. 100.

D. Statistical methods

Behavioural data were analyzed with non parametric analysis of variance (Siegel, 1956; Scheirer et al., 1976). A normal distribution of hormonal blood levels was tested by Shapiro & Wilk's test (1965). Group means were compared with classical parametric analysis of variance (LeLouch & Lazar, 1974). When repeated measures were made in the same animals, a split-plot design was used (Gill & Hafs, 1971). Post-hoc comparisons of group means used the Newman-Keuls test. Results are given as group means with standard error of the mean.

III. Results

A. Behavioural measures

Behavioural data collected in animals exposed to the new environment are shown in figure 1. The activity score was significantly influenced by both breed (Hm = 8.58; d.f. = 3; P < 0.05) and sex (Hm = 7.47; d.f. = 1; P < 0.01) with a non-significant interaction. The mean activity of females was higher (36 vs. 16 sections entered). The major interbreed difference was the lower activity of MS (median number of sections entered: 10.5). When compared to the other breeds (JX = 28.0; JH 17.5; crossbred 36.5). The other criteria were found to be less discriminant. A difference between breeds was observed in the number of grunts (Hm = 7.24; d.f. = 3; P < 0.10) and squeals (Hm = 8.16; d.f. = 3; P < 0.05), the sex factor and the interaction being non significant. MS pigs vocalized less than the other animals.

The results of the neophobia test are given in figure 2. Numerous animals displayed the maximal score of 5 mn, which reduces the significance of the results. Contact latencies did not differ between breeds (H'm = 0.75; d.f. = 3), unlike food intake latencies (H'm = 6.33; d.f. = 3) which were lower in Mei-Shan pigs.
Fig. 1

Individual scores of locomotor activity (number of sections entered) and vocalizations during the 10-min novel environment test, according to sex and breed [$MS = Mei-Shan, JX = Jia-Xing, JH = Jin-Hua (MS \times LR) LR = crossbred]$.

Activité motrice (nombre de carrés traversés) et vocalisations mesurées pendant le test d'environnement nouveau, selon le sexe et la race [$MS = Mei-Shan, JX = Jia-Xing, JH = Jin-Hua (MS \times LR) LR = croisés]$.
B. Endocrine results

Plasma ACTH and corticosteroids

Due to a log-normal distribution of plasma ACTH and corticosteroid levels in pigs, data were submitted to logarithmic transformation before statistical analysis (MORMÈDE & DANTZER, 1978 a).

— Basal levels (fig. 3). For blood cortisol levels, two-way analysis of variance indicated as non significant effect of the sex factor ($F(1.56 = 0.18)$ with a significant breed factor ($F(3.56) = 5.46 ; P < 0.01$). No difference was found between Chinese breeds but crossbred animals differed significantly from MS ($P < 0.05$), JX and JH ($P < 0.01$). Plasma ACTH levels differed according to sex ($F(1.56) = 7.38 ; P < 0.01$) and breed ($F(3.56) = 10.40 ; P < 0.001$) without interaction. Females had lower ACTH levels than males. The breeds were distributed in a regular way from crossbred with the lowest levels to JH with the highest.

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**Fig. 2**

*Individual scores of contact with the food trough and food intake latencies measured in the neophobia test. Same legend as figure 1.*

*Latence de contact avec l'auge et de prise de nourriture mesurée dans le test de nérophobie. Même légende que figure 1.*

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Fig. 3

Basal levels of blood ACTH and cortisol (on a logarithmic scale) according to sex and breed. Mean ± S.E.M., number of animals in brackets.

Taux de base d’ACTH et cortisol plasmatiques selon le sexe et la race.
Moyenne ± écart type de la moyenne, nombre d’animaux entre parenthèses.

Fig. 4

Hypophyse-adrenocortical response to the novel environment test.
Blood levels of ACTH and cortisol (on a logarithmic scale) before (time 0), at the end of the test (10 mn) and 20 mn later (30 mn). Mean ± S.E.M., 8 animals per group.
Réponses de l’axe hypophyse-corticosurrénalien au test d’environnement nouveau.
Concentrations plasmatiques d’ACTH et de cortisol mesurées avant (temps 0), à la fin du test (10 mn) et 20 minutes plus tard (30 mn). Échelle logarithmique.
Moyenne ± écart type de la moyenne.
Response to the novel environment test (fig. 4). The results of the analysis of variance are given in table 1. Exposure to the novel environment induced an increase in plasma ACTH and corticosteroid levels, the ACTH increase being larger in the breeds with the lowest initial levels (significant breed × period interaction). The interbreed differences in basal levels disappeared at the end of the test (F (3.28) = 1.71). Conversely, the differences seen in basal corticosteroid levels remained unchanged all along the test (non-significant breed × period interaction): crossbred pigs displayed lower levels of cortisol (P < 0.01) than purebred Chinese pigs.

Table 1

*Novel environment test - Plasma hormonal levels.*

*Results of the analysis of variance (split-plot design), F values.*

|                  | d.f. | Adrenaline | Noradrenaline | Cortisol | ACTH  |
|------------------|------|------------|---------------|----------|-------|
| **Between subjects** |      |            |               |          |       |
| Breed (A)        | 3    | 7.12c      | 4.30b         | 8.44d    | 5.94e |
| Sex (B)          | 1    | 4.16a      | 3.60a         | 0.31     | 2.16  |
| A × B            | 3    | 1.17       | 0.16          | 1.02     | 1.60  |
| Error            | 24   |            |               |          |       |
| **Within subjects** |      |            |               |          |       |
| Period (C)       | 2    | 5.08c      | 0.94          | 36.11d   | 34.07d|
| A × C            | 2    | 1.09       | 1.18          | 1.74     | 5.87d |
| B × C            | 2    | 0.63       | 1.64          | 0.37     | 0.00  |
| A × B × C        | 6    | 1.97       | 1.31          | 0.21     | 0.49  |
| Error            | 24   |            |               |          |       |

a P < 0.10.
b P < 0.05.
c P < 0.01.
d P < 0.001.

Dynamic test (fig. 5). The treatment factor (F (3.42) = 16.54 ; P < 0.001), the breed factor (F (2.21) = 23.34 ; P < 0.001) and their interaction (F (4.42) = 3.63 ; P < 0.05) were found to be significant. Dexamethasone lowered and ACTH increased plasma corticosteroid levels and their variations were larger in crossbred animals.
Plasma catecholamines

The hypothesis of a normal distribution of basal plasma adrenaline ($W = 0.832$; $N = 32$; $P < 0.01$) and noradrenaline ($W = 0.777$; $N = 32$; $P < 0.01$) levels was not confirmed by the Shapiro and Wilk's test. Conversely, the hypothesis of log-normal distributions could not be rejected ($W = 0.953$; $P < 0.10$ and $W = 0.975$; $P < 0.50$ respectively). Data were therefore submitted to logarithmic transformation prior to analysis.

Results obtained in the novel environment test are given in figure 6 and table 1. The breed factor was found to be significant. JX displayed lower adrenaline levels ($P < 0.01$) than the other three breeds and lower noradrenaline levels than either JH or crossbreds ($P < 0.05$). Females had generally lower levels than males but the difference was significant only for adrenaline in JX (63 vs. 129 pg/ml; (F(1.6) = 12.45;
P < 0.025). Adrenaline levels were found to be lower 20 min after the end of the test (P < 0.05) but noradrenaline levels did not change significantly over sampling times.

**IV. Interpretation and discussion**

**A. Behavioural testing**

The novel environment test and the neophobia test have already been used to assess reactivity of pigs from different breeds or with differential rearing experience (DANTZER & MORMÈDE, 1978, 1981a). These tests offer the advantage of enabling behavioural measurements in animals exposed to an environmental challenge while triggering the activity of their neuroendocrine systems (MORMÈDE & DANTZER, 1978a).

In the novel environment test, fearfulness is usually observed either as low activity (behavioural inhibition) or high activity (behavioural activation, usually associated with escape attempts) together with many squeals. According to this criterion, female JH
pigs would appear to be more reactive than crossbred pigs, while JX pigs are as reactive. Male JH pigs and MS pigs were characterized by a low level of activity associated with few vocalizations which would suggest that they were relatively indifferent to the new situation to which they had been subjected. In the case of MS pigs, this interpretation is further supported by their reduced reluctance to feed from the new trough in the neophobia test. In contrast, male JH pigs did not respond at all in this last test, suggesting that they have strong inhibitory tendencies in their behavioural repertoire.

Sexual dichotomy, with females exhibiting a higher activity score than males is a common feature in laboratory rodents (ARCHER, 1973). This dichotomy which is more strikingly pronounced in JH pigs than in other breeds is not observed in any of the European breeds and their crossbred products we have tested so far, though it has been observed in other behavioural tests such as avoidance of electric shocks (DANTZER & MORMÈDE, 1978). Its possible origin will be discussed later, together with sex related endocrine differences.

B. Plasma catecholamines

Few data are available in the literature for us to compare plasma catecholamine levels. Using a similar radioenzymatic assay, BARRAND et al. (1981) found lower levels in a catheterized pig (80-180 pg/ml and 10-30 pg/ml for noradrenaline and adrenaline respectively). The exquisite sensitivity of plasma catecholamine levels to handling related to blood sampling has been shown in laboratory species (BUHLER et al., 1978 ; MC CARTY et al., 1981) and the values obtained here are probably not true « basal » levels, blood samples being obtained by direct venous puncture in the awake animal. However, the difference is not related exclusively to sampling techniques ; JX pigs displayed low plasma CA levels, close to those published by BARRAND et al. (1981), so that the breed factor may be of major importance. Such inter-breed differences have already been published for rats (MC CARTY & KOPIN, 1978), for both basal and stress levels.

Noradrenaline levels were regularly found to be higher than adrenaline levels (overall mean 350 ng/ml vs. 200 ng/ml), which has already been shown by BUHLER et al. (1978) in numerous mammalian species.

There was no evidence of an increase in plasma catecholamine levels as a consequence of exposure to the new environment. It has already been shown in rats that plasma catecholamine levels are not sensitive to such a stimulus (MC CARTY & KOPIN, 1978 ; NATelson et al., 1981) which is in contrast to the exquisite sensitivity of the pituitary-adrenal axis (PFISTER, 1979).

C. Pituitary-adrenal axis

The influence of sex and breed on activity and reactivity of the pituitary-adrenal axis has been little studied in farm animal species.

We have been unable to find sex-related differences in ACTH and glucocorticoid levels in immature pigs of the European breeds Pietrain and Large White (MORMÈDE
In accordance with data already published by Dvorak (1972) for plasma 11-hydroxycorticosteroid levels. Sex differences in adrenocortical axis activity and reactivity are well documented in laboratory rats. The amplitudes of the daily corticosterone cycle (Critchlow et al., 1963) and the hypophyso-adrenocortical response to stress (Barrett, 1960; Le Mevel et al., 1978) are larger in the female rat. Dexamethasone blockade is also less effective in females (Ramaley, 1976). All these characteristics disappear after castration and are absent before sexual maturity. Oestradiol seems to be responsible for these effects (Barrett, 1960; Kitay, 1963a; Schleim et al., 1974). Conversely, male sexual hormones exert a tonic inhibition on pituitary-adrenal activity, which can be removed by gonadectomy (Kitay, 1963b; Lescoat, 1981). Since sexual differences in pituitary-adrenal activity are acquired during the course of sexual maturation (Lescoat, 1982) and since Chinese breeds have an earlier sexual maturity [81, 91 and 109 days in MS, JX and JH pigs respectively vs. 210 days in Large White pigs for instance (Legault & Caritez, 1982; Legault & Gruand, 1981)], it is possible that the discrepancies between the present results and our previous data come from differences in the developmental stage of the endocrine system at the time of testing. As an alternative hypothesis, the existence of a structural difference between European and Chinese breeds cannot be ruled out until further studies of adult animals from both origins are carried out.

Interbreed differences in the pituitary-adrenal axis have already been described in pigs (Aberle et al., 1976; Marple et al., 1972; Mormede & Dantzer, 1978). These differences were initially attributed to stress susceptibility, as defined by sensitivity to sudden death syndrome or reactivity to halothane anesthesia, stress-susceptible breeds having higher ACTH levels with unchanged corticosteroid levels (Marple et al., 1972). However, this difference was no more evident when comparing halothane positive and negative littermates (Mormede & Dantzer, 1978). It is worth noting that the variations of plasma ACTH levels by Marple et al. (1972) were far larger than plasma corticosteroid changes and were not related to them, confirming the present results of an apparent dissociation between blood ACTH and corticosteroid levels. Strain differences in adrenocortical activity are well documented in laboratory rodents (Crabbe et al., 1981; Gentsch et al., 1981; Levine & Treiman, 1964; Popova & Koryakina, 1981). Popova & Koryakina (1981) gave evidence for a central origin of the inter-strain differences of adrenocortical activity in mice. They found that the stress responses were related to basal levels of corticosteroids, but this was not the case for the adrenocortical response to ACTH. Furthermore, Brown & Nestor (1973) and Edens & Siegel (1975) showed in poultry that the adrenal response to ACTH was a main target for selection pressure on the corticosterone stress response, so that different elements of the hypophyso-adrenocortical axis may be involved in determining the differences observed in selected breeds or lines. The adaptive significance of such inter-breed variations in endocrine activities has to be considered in the light of behavioural results.

Lastly, the dissociation between ACTH and corticosteroid levels was not completely unexpected. A growing body of evidence suggests that both the pituitary hormone ACTH and the adrenocortical glucocorticoids are not so tightly linked as was previously assumed (Wood et al., 1982). Nevertheless, further work is necessary to find out the exact nature of the link between them.
D. Hormone - Behaviour relationships

Endocrine and behavioural response to threatening stimuli are two components of the highly integrated adaptive response to environmental changes (see review in DANTZER & MORMÈDE, 1983). Evidence for this integration is threefold: correlation between hormones and behaviour (DANTZER et al., 1980), influences of hormones on behavioural responses (MORMÈDE & MORMÈDE, 1978 b) and influence of behavioural strategies on neuroendocrine activities (DANTZER & MORMÈDE, 1981 b). The compelling evidence in favour of such hormone-behaviour interrelationships prompted us to look more closely at the influence of inter-breed differences on those relationships.

Basal ACTH levels and mean adrenaline levels were plotted against locomotor activity in the novel environment for the eight groups (sex X breed) under study (fig. 7). In both cases, JX females were very different from other groups, so that they are excluded from this interpretation and their case will be discussed separately.

When considering ACTH-activity relationships, a highly significant negative correlation was found ($r = -0.925$; d.f. = 5; $P < 0.01$). The same negative correlation ($r = -0.986$; d.f. = 3; $P < 0.02$) was found in Chinese pigs for the adrenaline-activity relationship, the two crossbred groups being displaced towards higher loco-

**FIG. 7**

*Correlations of mean blood ACTH levels (basal conditions) and blood adrenaline levels with locomotor activity in the novel environment test, according to sex and breed (both axes are on a logarithmic scale). Mean ± S.E.M., 4 animals per group.*

*Corrélations entre les concentrations plasmatiques d’ACTH en conditions de base (à gauche) ou les concentrations moyennes d’adrénaline (à droite) et l’activité motrice mesurée dans le test d’environnement nouveau, selon le sexe et la race.*

*Les deux échelles sont logarithmiques.*

*Moyenne ± écart type de la moyenne, 4 animaux par groupe.*
motor activities in a roughly parallel manner. These results suggest that at least three hormonal factors may influence behavioural activity in a threatening situation: an ACTH and an adrenaline factor are readily apparent in figure 7. The possible intervention of a corticosteroid factor is suggested by the orthogonal displacement of the adrenaline-activity relationship curve from Chinese pigs with high levels of corticosteroids and low levels of corticosteroids and high motor activity.

Hormone-behaviour relationships have been completely unexplored in farm animals up to now, so that these results have to be compared with the data available in the literature on laboratory animal species. The relation between plasma ACTH and behavioural activity in the open-field has not been described, plasma corticosterone being the representative variable generally used to assess pituitary-adrenal activity. This is unfortunate since our results clearly show that both hormones convey different information. In rats, basal (File & Velucci, 1979) or post-stress (Gentsch et al., 1981) plasma corticosterone levels have been found to be associated with low motor activity in an open-field situation. Conversely, a high behavioural reactivity has been shown to be associated with a high catecholamine release in blood (Mc Carty & Kopin, 1978; McCarty et al., 1979; Gilad & Jimerson, 1981). These results are in full agreement with Henry's hypothesis of a preferential activation of catecholaminergic systems in the case of active responding and of the pituitary-adrenocortical system in conservation-withdrawal types of responding (Henry, 1982).

We suggest here that an adrenocortical factor and a sympathetic factor combine to influence the open-field activity. In rats, a high adrenocortical tone and a low sympathetic tone are associated with low active responding. This combination is obvious in the results of Gentsch et al. (1981): the correlation between motor activity and corticosterone is displaced towards higher motor activity levels in those strains known or supposed to have higher sympathetic tone. The same line of reasoning is valid here with the noticeable difference that a high sympathetic tone is associated with a low motor activity in the open-field. In contrast, a high adrenocortical activity is related in both rats and pigs to low motor activity. Similarly, high blood corticosterone levels were found in chickens selected for low activity in the open-field (Faure, 1981).

Female JH do not fit into this framework, suggesting that other still unknown factors may be of importance in these hormone-behaviour relationships. Among other hormonal factors, the influence of sex hormones should be investigated.

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