Prolactin-Enhanced Grooming Behavior: Interaction with ACTH

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The interaction between prolactin (PRL) and ACTH in enhancing grooming behavior after intracerebroventricular (i.c.v.) administration was investigated in intact and endogenously hyperprolactinaemic rats. In intact rats, 4 h after the i.c.v. injection of rat PRL or ACTH, a subsequent administration of ACTH or rat PRL did induce similar excessive grooming as observed after the first injections. In hyperprolactinaemic rats, which displayed excessive grooming 12 days after homografting adenopituitaries under the kidney capsule, i.c.v. injection of rat PRL failed to enhance further the grooming activity while this behavior was substantially enhanced by i.c.v. injection of ACTH₁₋₂₄. Twenty-six days after surgery, when the grooming activity of hyperprolactinaemic rats was at the same level as control animals, the i.c.v. injection of rat PRL was effective in inducing excessive grooming in control but not in hyperprolactinaemic animals. In contrast, at this time the i.c.v. injection of ACTH₁₋₂₄ induced again excessive grooming in both hyperprolactinaemic and control rats. Accordingly, there was no cross-tolerance between PRL and ACTH in inducing excessive grooming, but hyperprolactinaemic rats became hyposensitive to exogenous PRL.

It is suggested that although PRL and ACTH may affect common neurotransmitter systems in the brain, the two hormones probably act on independent neural mechanisms in inducing excessive grooming in the rat.

INTRODUCTION

The adenohipophyseal hormones prolactin (PRL) and corticotropin (ACTH) can enhance grooming behavior in the rat^{5,6,14}. There is evidence suggesting that both peptides induce excessive grooming by interacting with dopamine and opioid transmission in the brain. Either systemic or intrastriatal injection of the dopamine receptor antagonist haloperidol suppresses both PRL^{6,7} and ACTH-enhanced grooming behavior²⁹. Furthermore, the peptide-enhanced grooming activity can be antagonized by systemic injection of the opiate receptor blocker naloxone^{9,30}.

Despite of these similarities, there are differences between PRL- and ACTH-induced excessive grooming. PRL-enhanced grooming is accompanied by a slight increase in the percentage of genital grooming (ref. 5), while ACTH does not modify the composi-

tion of grooming as compared to that of control animals¹³. Furthermore, high levels of plasma PRL as induced by pituitary homografts under the kidney capsule are accompanied by excessive grooming^{5,6}, while ACTH only promotes vigorous grooming after intracerebroventricular (i.c.v.) administration¹³.

In the present paper, two attempts were made to investigate whether PRL and ACTH interact in inducing excessive grooming. After determining the dose-response curve of PRL-induced excessive grooming after i.c.v. injection, we have studied the effects of a previous i.c.v. administration of PRL or ACTH on the grooming activity elicited by a subsequent injection of ACTH or PRL in order to determine whether cross-tolerance develops between the two peptides. In the third experiment the grooming response induced by i.c.v. administration of PRL or ACTH in hyperprolactinaemic rats was examined.

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MATERIALS AND METHODS

Animals and surgery

Male rats of Wistar strain, weighing approximately 150 (± 10) g were used. They were kept under a constant light-dark cycle (lights on between 8.00 and 20.00 h) with food and water ad libitum. All animals, anesthetized with Hypnorm (Philips-Duphar B.V., Amsterdam), were implanted with a plastic cannula inserted into the brain ventricular system (foramen interventriculare²). In addition, a group of rats received a homograft of two adenopituitaries under the kidney capsule according to the method described by Welsch et al.²⁷ during the same surgery session. The sham-operated group received a smooth muscle graft under the kidney capsule.

Behavioral procedures

Grooming activity of the rats was scored as described by Gispen et al.¹⁴. Briefly, the rats were placed individually into boxes with transparent walls (1 $\times$ 1 $\times$ h, 24 $\times$ 12 $\times$ 24 cm) in a low-noise room. The behavior of the rats was sampled every 15 s beginning immediately after the animals were placed into the boxes. The occurrence of grooming was recorded for 35 or 50 min, with a maximum of 140 and 200 possible positive grooming scores, respectively.

Experimental design

In the first series of experiments a group of 33 cannulated intact rats was used for determining the dose-response curve of the PRL-induced excessive grooming. The animals were tested one week after surgery. A highly purified preparation of rat PRL (rat PRL RP1, NIAMDD, U.S.A.) was used. It showed a potency of 11 IU/mg (mouse deciduoma assay). Rat PRL was dissolved in saline and injected i.c.v. at different doses: 1, 3, 5, and 10 μ g/3 μ l/rat. Grooming rating started 15 min after injection and lasted 50 min.

The second experiment was designed to study the cross-tolerance between PRL- and ACTH-induced excessive grooming as described by Jolles et al.¹⁸. For this experiment the dose of 3 μ g of rat PRL was selected on the basis of the dose-response relationship obtained in the first experiment. The dose of 0.3 μ g of ACTH₁₋₂₄ was selected being optimally effective in inducing excessive grooming¹³. Rat PRL

and ACTH₁₋₂₄ (Organon, Oss, The Netherlands) were dissolved in saline and injected i.c.v. A group of 18 cannulated experimentally naive rats were used. Rat PRL (3 μ g/3 μ l/rat), ACTH₁₋₂₄ (0.3 μ g/3 μ l/rat) or saline were injected i.c.v. and the grooming rating was started 15 min later. After the observation session of 50 min the rats were returned to their homecages. Four hours after the first injection, ACTH₁₋₂₄ (0.3 μ g/3 μ l/rat) was administered i.c.v. to those animals which were previously given PRL, and rat PRL (3 μ g/3 μ l/rat) to those which previously received ACTH₁₋₂₄. Furthermore, the control group was again injected with saline. Grooming behavior was recorded for 50 min, starting 15 min after treatment.

In the third experiment homografted and sham-operated rats were tested for grooming activity every other day from the second until the twenty-sixth postoperative day, between 15.00 and 19.00 h, under the same environmental conditions. Each observation session lasted 35 min. The grooming activity of homografted rats reached the highest level on the twelfth postoperative day and subsequently declined until normalization on the twenty-sixth day after surgery, as already described⁵. In order to study the influence of i.c.v. administration of PRL and ACTH on the highest and lowest grooming level of homografted rats, on twelfth and twenty-sixth day after surgery grooming behavior was scored 15 min after the i.c.v. injection of saline, rat PRL (3 μ g/3 μ l/rat) or ACTH₁₋₂₄ (0.3 μ g/3 μ l/rat).

At the end of behavioral procedures all animals were killed by decapitation. Localization of intraventricular cannulas was checked by injecting Evans blue and macroscopical inspection of the colouring of the walls of the ventricular system in formaline-fixed brains. Radioimmunoassay (RIA) of plasma PRL levels in homografted and sham-operated animals was performed as described by Niswender et al.²¹, using NIAMDD rat PRL as reference. All samples were processed in duplo in 6 serial 1:2 dilutions.

Statistical analysis

Statistical analysis was made using Student's *t*-test (two-tailed), and the Dunnett-test (multiple comparisons). A probability level of 0.05 or less was accepted as a significant difference.

RESULTS

The post-mortem control revealed that all cannulas were correctly implanted into the ventricular system of the rats. Twenty-six days after operation, plasma PRL levels of homografted animals, as measured by RIA, were significantly higher than those of sham-operated controls (76.05 ± 3.01 ng/ml, $n = 12$, vs 17.81 ± 1.35 ng/ml, $n = 11$, $P < 0.001$, Student's t -test, two-tailed).

Fig. 1 shows the dose-response curve of PRL-induced excessive grooming after i.c.v. administration. Significant enhancement of grooming occurred following i.c.v. administration of rat PRL in all the doses tested, but an inverted U-shape dose-response relation was found. The highest level of grooming was observed at the dose of $3 \mu\text{g}$ of rat PRL. Both higher and lower doses were less effective than $3 \mu\text{g}$ of rat PRL in inducing excessive grooming.

In the second experiment that was designed to study cross-tolerance, i.c.v. injection of both rat PRL ($3 \mu\text{g}/3 \mu\text{l}/\text{rat}$) and ACTH_{1-24} ($0.3 \mu\text{g}/3 \mu\text{l}/\text{rat}$) resulted in increased grooming activity. Administration of ACTH_{1-24} i.c.v. 4 h after PRL injection resulted in the same increase in grooming activity as it was observed in rats that received ACTH_{1-24} as first treatment. Similarly, PRL-induced enhancement of grooming in rats which were treated first with ACTH_{1-24} was in the same order of magnitude as in rats receiving PRL as first injection (Table I).

Fig. 1. Enhancement of grooming behavior by graded doses of rat PRL administered intracerebroventricularly. Significance of differences vs saline-injected control rats ($n = 8$) was calculated by means of Dunnett's parametric multiple comparison test: * $P < 0.05$; ** $P < 0.01$. Figures in columns represent the number of observations.

TABLE I

Effects of intracerebroventricular injection of rat PRL and ACTH_{1-24} on the enhancement of grooming behavior by a subsequent intracerebroventricular injection of rat PRL or ACTH_{1-24}

Rat PRL ($3 \mu\text{g}$) and ACTH_{1-24} ($0.3 \mu\text{g}$) were administered in $3 \mu\text{l}$ of saline. Data show mean $\pm$ S.E. of 6 observations per treatment.

	Grooming score		
	PRL	ACTH	Saline
First injection	$110.4 \pm 12.6^*$	$124.6 \pm 24.4^*$	23.8 ± 2.5
Second injection	$118.7 \pm 24.9^*$	$110.1 \pm 21.9^*$	26.9 ± 2.3

* Significance of difference ($P < 0.01$, Dunnett-test) vs saline-treated rats.

On the twelfth day after operation the grooming behavior of pituitary homografted rats was significantly higher than that of sham-operated animals ($P < 0.01$, Student's t -test, two-tailed). Administration of rat PRL i.c.v. ($3 \mu\text{g}/3 \mu\text{l}/\text{rat}$) in sham-operated rats increased grooming behavior to a level similar to that of homografted animals injected with saline. However, i.c.v. administration of PRL failed to increase further the level of grooming activity in homografted animals. In contrast, the grooming

Fig. 2. Effects of intracerebroventricularly administered rat PRL ($3 \mu\text{g}$) and ACTH_{1-24} ($0.3 \mu\text{g}$) on the grooming behavior of rats bearing pituitary homografts (shaded columns) or of sham-operated animals (open columns). The observations were carried out 12 and 26 days after operation. Significance of differences vs saline-injected sham-operated rats were calculated by means of Dunnett's parametric multiple comparison test: * $P < 0.05$; ** $P < 0.01$. Figures in columns represent the number of observations.

scores of both sham-operated and homografted rats injected with ACTH₁₋₂₄ (0.3 µg/3 µl/rat) were significantly higher than those of animals injected with PRL ($P < 0.01$, Student's *t*-test, two-tailed) (Fig. 2). By the twenty-sixth day after surgery, the grooming behavior of homografted rats was not different from that of sham-operated animals. The i.c.v. administration of PRL in sham-operated animals increased significantly their grooming response, whereas it failed to increase that of homografted rats. Furthermore, both homografted and sham-operated rats exhibited excessive grooming after i.c.v. injection of ACTH₁₋₂₄. The grooming scores were significantly higher than in their saline-treated controls, but also higher than in sham-operated rats receiving rat PRL ($P < 0.01$, Student's *t*-test, two-tailed).

DISCUSSION

Both adenohipophyseal hormones PRL and ACTH induce excessive grooming in the rat^{5,6,13}. PRL-enhanced grooming behavior can be elicited either by intracerebral injection of rat PRL^{6,7} or by endogenous hyperprolactinaemia as induced by pituitary homografts under the kidney capsule^{5,6}. These homografts, disconnected from the normally operating hypothalamic control, secrete high levels of PRL, and very little, if any of other hypophyseal hormones^{5,20}. It is therefore likely that PRL or fragments of this hormone are responsible for the increased grooming activity of homografted rats.

Of all doses of rat PRL tested after i.c.v. injection, the most effective appeared to be 3 µg. The dose-response curve of PRL-enhanced grooming is of an inverted U-shape type. This type of dose-response curve is not uncommon for peptide-brain interaction^{15,28}. As only grooming behavior was recorded, it may be that other competing behaviors are responsible for the lowered effectiveness of doses higher than 3 µg of rat PRL. This seems to be the case of opioids¹³ and opiate-like peptides such as β-endorphin³¹. Interestingly, excessive grooming induced by exogenous rat PRL or short-term hyperprolactinaemia involves opioid components. The opiate receptor antagonist naloxone markedly reduced PRL-induced grooming⁹. The dose-range for PRL-enhanced grooming after i.c.v. administration is apparently 10 times higher than that found

for the excessive grooming induced by ACTH₁₋₂₄¹³. However, the molecular weight of PRL is 10 times larger than that of ACTH₁₋₂₄ and thus on a molecular basis the difference is only small. The dose of 3 µg of rat PRL being optimally effective in inducing excessive grooming was selected for the cross-tolerance study.

Repeated i.c.v. injections of ACTH₁₋₂₄ (1 µg/rat) result in a reduction of grooming behavior elicited by the second injection¹⁸. This single dose tolerance has been found when the second administration of the hormone was performed between 1 and 8 h after the first one, and it disappeared when the interval between the two injections was 18 h or more^{3,18}. In the study of single-dose tolerance to peptide-induced grooming, a 4-h interval between the first and second injection is usually used¹³. In the present experiments we have performed the second administration of PRL and ACTH 4 h after the first injection. No single-dose tolerance was observed between PRL and ACTH suggesting that not the same putative receptor mechanisms are involved. Moreover, no doses higher than 3 µg of rat PRL could be used since the dose-response curve was inverted U-shaped and 3 µg in our hands was the most active dose of rat PRL.

Administration of PRL i.c.v. failed to affect grooming activity in hyperprolactinaemic rats, whether the base-line grooming activity was high (day 12) or low (day 26 of hyperprolactinaemia). In contrast, i.c.v. injection of ACTH enhanced further the grooming activity of hyperprolactinaemic animals whenever after pituitary implantation it was performed. Accordingly, hyperprolactinaemic rats were non-responsive to exogenous PRL under all conditions tested here, but responsiveness to ACTH was preserved. The ineffectiveness of exogenous PRL in hyperprolactinaemic rats may mean that neural structures involved in PRL-induced grooming became tolerant to PRL or at least desensitization occurred. That an increased exogenous PRL level and not the base-line grooming activity is of importance in this phenomenon is suggested by the finding that plasma PRL level is already high 12 days after pituitary transplantation⁵. Desensitization of some neural elements in relation to long-term hyperprolactinaemia have already been reported. Beck and Wuttke¹ found desensitization of dop-

amine-sensitive mechanisms that are inhibitory to LH-RH release. It should be mentioned, however, that such tolerance or desensitization occurs only in grooming⁵ and sexual¹⁰ but not in other behaviors such as active avoidance acquisition or responsiveness to electrical footshock¹⁰. Furthermore, certain dopaminergic systems may be supersensitive to dopamine agonists such as amphetamine or apomorphine⁸.

These results, taken together, suggest that PRL- and ACTH-induced excessive grooming probably involve independent neural mechanisms, despite similar localization of their site of action, i.e. in the substantia nigra^{7,29}. Furthermore, it seems that central mechanisms responsible for grooming behavior become tolerant to PRL in long-term hyperprolactinaemia, whereas they are still sensitive to ACTH. The results are consistent with data showing that PRL- and ACTH-enhanced grooming are qualitatively different^{5,13}, and that endogenous hyperprolactinaemia also enhances grooming activity^{5,6} while ACTH only promotes excessive grooming after i.c.v. administration¹³. However, it remains to be shown which neural substrate mediates primarily PRL- and ACTH-induced excessive grooming. Both PRL^{12,22,23} and ACTH^{11,16,24,26} affect dopaminergic and opioid mechanisms in the brain. Dopamine and opioid receptors seem to be involved in both PRL-^{7,9}

and ACTH-induced excessive grooming^{29,30}. Yet, these peptides also seem to affect other neurotransmitter systems in the brain, such as norepinephrine, serotonin and GABA^{17,19,26,30}.

Indeed, it has been recently shown that clonidine, a potent α_2 -receptor agonist¹³ and anti-depressant drugs, such as amitriptyline and nomifensine²⁵ reduced ACTH-induced excessive grooming. Although the present experiments do not allow a firm conclusion, they suggest that the neuropharmacology of PRL- and ACTH-induced grooming is more complex than the proposed dopaminergic system containing opiate-sensitive component alone^{4,7,9,13,30}.

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