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TIME COURSE OF CHANGES IN BRAIN SEROTONERGIC ACTIVITY AND BRAIN TRYPTOPHAN LEVELS IN DOMINANT AND SUBORDINATE JUVENILE ARCTIC CHARR

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Summary

Concentrations of serotonin (5-HT), 5-hydroxyindoleacetic acid (5-HIAA) and tryptophan (TRP, the amino acid precursor of 5-HT) were measured, and 5-HIAA/5-HT ratios calculated, in the telencephalon, hypothalamus and brain stem of Arctic charr (*Salvelinus alpinus*) with 1–21 days experience of a dominant or subordinate position in a pair. Brain 5-HIAA levels and 5-HIAA/5-HT ratios (an index of serotonergic activity) increased rapidly in all three areas of the brain in subordinate fish and remained high for up to 21 days. The brain stem 5-HIAA concentration in dominant fish showed a temporary increase after 1 day of social interaction, but returned to the control level 2 days later. The social interactions did not affect 5-HT concentrations in any of the brain regions. An initial, but temporary, increase in brain TRP concentration was seen in both subordinate and dominant fish. After 1–3 days of social interaction, brain TRP levels declined. This decline was most pronounced in subordinate individuals which, after 7 and 21 days, had hypothalamic TRP concentrations significantly lower than those of controls. Moreover, TRP levels in the telencephalon after 21 days, and in the hypothalamus after 7 days, were significantly lower in subordinate individuals than in dominant fish. These results show that subordinate experience rapidly causes a sustained increase in brain 5-HT metabolism which does not correlate with changes in brain TRP levels. Thus, the increases in brain 5-HIAA concentration and in brain 5-HIAA/5-HT ratios probably reflect an increase in functional 5-HT release, a phenomenon that appears to have a wide distribution in the brain.

Introduction

When held in small groups, juvenile Arctic charr (*Salvelinus alpinus*) develop an essentially linear dominance hierarchy, in which the dominant fish is the most aggressive and usually the largest individual (Noakes, 1980).

In previous studies of Arctic charr, we have found that low positions in a dominance hierarchy are associated with increased levels of 5-hydroxyindoleacetic acid (5-HIAA), the main metabolite of serotonin (5-hydroxytryptamine, 5-HT), in both the telencephalon and brain stem, with social rank being inversely correlated with both the brain 5-HIAA

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concentration (Winberg *et al.* 1991) and the 5-HIAA/5-HT ratio (Winberg *et al.* 1992*a*), an index of serotonergic activity (Shannon *et al.* 1986). Furthermore, we have shown that this increase in serotonergic activity in subordinate fish is socially induced (Winberg *et al.* 1992*b*).

Subordinate individuals show much lower growth rates than dominant fish (Abbott and Dill, 1989; Winberg *et al.* 1992*b*), probably as a result of stress as well as a reduced food intake, since fish occupying a low position in a dominance hierarchy suffer from increased stress (Noakes and Leatherland, 1977; Ejike and Schreck, 1980; Peters *et al.* 1980; Scott and Currie, 1980).

In mammals, both stress (Bliss *et al.* 1972; Curzon *et al.* 1972; Morgan *et al.* 1975; Morgan and Rudeen, 1976; Adell *et al.* 1988; Mitchell and Thomas, 1988) and starvation (Curzon *et al.* 1972; Kantak *et al.* 1978; Fuenmayor and Garcia, 1984) have been reported to increase brain serotonergic activity. We recently found that repeated artificial stress increases brain 5-HIAA concentrations and 5-HIAA/5-HT ratios in Arctic charr, while starvation *per se* has no effect on brain 5-HT utilization (Winberg *et al.* 1992*b*). Thus, stress is likely to be a factor underlying the increase in brain serotonergic activity seen in subordinate fish.

Tryptophan (TRP) is the amino acid precursor of 5-HT. The rate of 5-HT synthesis is normally restricted by TRP availability in mammals (Boadle-Biber, 1982). In rainbow trout (*Oncorhynchus mykiss*), increased dietary TRP increases brain 5-HT and 5-HIAA levels (Johnston *et al.* 1990), indicating that the rate of 5-HT synthesis can also be dependent upon TRP availability in fish.

Interestingly, stress has been reported to increase brain TRP concentrations in mammals (Curzon *et al.* 1972; Neckers and Sze, 1975; Dunn, 1988; Dunn and Welch 1991). TRP is an essential amino acid, so plasma as well as brain TRP levels may depend on dietary factors. Consequently, because subordinate fish often have a greatly reduced access to food, the possibility arises that a subordinate position will result in decreased brain levels of TRP. However, the time course of changes in brain 5-HT metabolism during hierarchic behaviour in fish has never been studied, nor have possible changes been related to brain TRP concentrations.

The aims of the present study are to investigate the time course of socially induced changes in brain serotonergic activity and to examine the possible relationships between levels of TRP, 5-HT and 5-HIAA in brains of Arctic charr. Concentrations of TRP, 5-HT and 5-HIAA were measured in telencephalon, hypothalamus and brain stem of fish with 1–21 days experience of a dominant or subordinate position in a pair.

Materials and methods

Fish

The fish (weighing 45.7±5.8g, mean ± S.D., *N*=78) were 2-year-old juvenile offspring of Arctic charr (*Salvelinus alpinus* L.) caught in lake Hornavan, Lapland, Sweden. They were kept indoors at the Department of Zoophysiology, in a holding tank continuously supplied with aerated Uppsala tapwater (8–11˚C) for more than 1 year before the experiment. The light:dark regime was continuously and automatically adjusted to conditions at latitude 51°N. The fish were fed daily with commercial trout pellets (EWOS ST40, Astra-EWOS, Sweden) at 2–4% of body weight.

Observation aquaria

Behavioural observations were made in four glass aquaria (1000mm × 500mm × 500mm) continuously supplied with aerated Uppsala tapwater ($0.80\,\mathrm{l\,min^{-1}}$, 8–10°C). Each aquarium was divided into four 50l chambers by inserting black polyvinylchloride (PVC) walls, and one fish was put in each of these chambers. In this way, each fish was kept visually isolated from other fish for 7 days in an attempt to diminish the effect of previous hierarchic experience. A black nylon-mesh screen was attached to the front side of the aquaria to minimize disturbance of the fish during observation. The remaining sides of the aquaria were covered with black plastic. Light was provided by fluorescent tubes (2 × 20W, warm white), placed 100mm above the water surface. The photoperiod was 12h:12h L:D with light on between 7:00 and 19:00h.

Experimental protocol

Fish were fed (approximately 3% of their body fresh weight) once a day by hand, both during the initial isolation period and during pair-rearing.

After the 1-week isolation period fish were put together in pairs, at 17:00h, by removing the PVC wall that had kept them separated. Fish in a pair were approximately equal in size, the mean mass difference being 3.8±3.2% (mean ± S.D., N=34). The fish were kept together for 1, 3, 7 or 21 days. Control fish (time=0) were isolated for 7 days in the same way as experimental fish, but were not allowed to interact with other fish. Aggressive acts in the pairs were counted during 4–6 sessions each of 15min. The first observation was made 5–10min after the fish had been put together in pairs and the last immediately before killing the fish. The types of behaviour patterns considered to be aggressive were attack (where the fish makes a rapid approach, often culminating in a bite), charge (a direct but slow approach towards the other individual) and nip (a bite without a prior approach).

Tissue sampling

At the end of each experimental period, between 17:00 and 18:00h, fish were decapitated. The brain of each fish (excluding olfactory bulbs and pituitary gland) was rapidly removed and divided into three parts: the telencephalon (weighing 12.9±2.3mg, mean ± S.D., N=78), hypothalamus (weighing 7.8±2.5mg, mean ± S.D., N=78) and the remaining parts of the brain (weighing 160.7±1.6mg, mean ± S.D., N=78), here denoted brain stem. The brain samples were wrapped in aluminium foil, frozen in liquid nitrogen (within 2min of decapitation) and kept at −80°C. Each fish was weighed after tissue sampling.

Assay of 5-HT, 5-HIAA and TRP

The frozen brain samples were homogenized in 4% (w/v) ice-cold perchloric acid containing 0.2% EDTA, 0.05% sodium bisulphite and $40\,\mathrm{ng\,ml^{-1}}$ epinine (deoxyepinephrine, the internal standard), using a Potter-Elvehjem homogenizer (brain stem), or a MSE 100 W ultrasonic disintegrator (telencephalon and hypothalamus).

5-HT and 5-HIAA were quantified using high performance liquid chromatography (HPLC) with electrochemical detection, as described by Nilsson (1989). TRP was analyzed using the same HPLC system by setting the detector on a higher oxidizing potential (1.0V instead of 750mV). As a measure of serotonergic activity, the 5-HIAA/5-HT ratio was calculated for each individual (Shannon *et al.* 1986; Winberg *et al.* 1991).

In 21 out of 234 samples (five telencephalon, eight hypothalamus and eight brain stem samples), unknown peaks interfered with the chromatograms, preventing the qualification of TRP.

Statistics

All data are presented as means ± S.E.M. Data were first compared using Kruskal–Wallis analysis of variance. If significant ($P<0.05$) differences were indicated by this test, individual groups were compared using the two-tailed Mann–Whitney *U*-test. When initial and final masses were compared, a paired Wilcoxon rank-sum test was used. Correlations were tested using Pearson correlation coefficients.

Results

Agonistic behaviour

When the first observation was made 5–10min after the fish had been put together in pairs, vigorous fighting was seen between most of the pairs. After 1–2h one individual in each pair, designated the subordinate, generally took a position close to the surface. Thereafter the subordinate fish spent most of the time in this position or in a corner of the aquarium. From this time onwards aggressive acts were almost exclusively performed by the dominant individual, which moved freely around the aquarium, usually close to the bottom. The dominance relationship determined during the first observation did not, in any case, differ from the one observed at intermediate time points or the relationship seen immediately before the fish had been killed.

Growth

Initially the fish were size-matched, although a small difference in mass was unavoidable. In 21 out of 34 pairs the largest fish became dominant ($P=0.23$, two-tailed binomial test). At the end of the experimental period, the dominant fish always had the highest mass. Dominant individuals showed a significant increase in mass after 3 and 21 days of pair-rearing, relative to individual starting mass (Fig. 1). Subordinate fish, however, lost weight and a significant decrease in mass, compared to individual starting mass, was found after 1, 3, 7 and 21 days of exposure to a dominant conspecific (Fig. 1). Control fish had gained weight during the 7 days of isolation (Fig. 1).

Brain levels of TRP, 5-HT and 5-HIAA

5-HIAA levels

5-HIAA concentrations rapidly increased in all three brain parts of subordinate fish

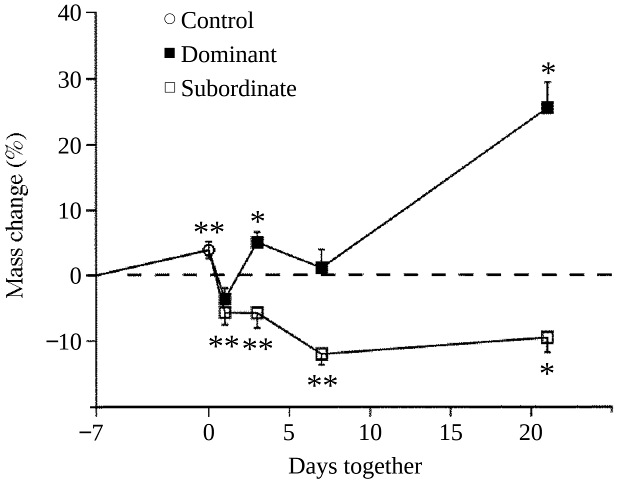

Fig. 1. Mass change, as a percentage of the initial mass (mass at day −7), in Arctic charr having 1, 3, 7 or 21 days experience of a dominant or subordinate position in a pair. The fish were weighed and isolated 1 week prior to the experiment. Fish that had been isolated for 1 week were used as controls. Values are means and S.E.M. from 7–10 individuals. $^*P<0.05$, $^{**}P<0.01$, rank-sum test (paired).

(Fig. 2A–C), and after 1 day of social interaction, significant differences were found in telencephalon and brain stem 5-HIAA levels between subordinate individuals and controls (Fig. 2A,C). Moreover, in brain stem, there was a significant increase in the 5-HIAA concentration in fish that had been dominant for 1 day. However, brain stem 5-HIAA levels in fish having a longer experience of being in a dominant position did not differ significantly from those in control fish (Fig. 2C), while the brain 5-HIAA concentrations of subordinate individuals remained high after longer periods of pair-rearing. Thus, significant differences in 5-HIAA levels between dominant and subordinate fish were found in the telencephalon after 3, 7 and 21 days (Fig. 2A), in the hypothalamus after 7 and 21 days (Fig. 2B) and in brain stem after 1, 3, 7 and 21 days of pair rearing (Fig. 2C).

5-HIAA/5-HT ratios

5-HIAA/5-HT ratios increased rapidly in the telencephalon, hypothalamus and brain stem of subordinate fish and differed significantly both from controls and from dominant individuals at all sampling times (Fig. 3A–C). In contrast, the brain 5-HIAA/5-HT ratios appeared to remain almost constant in dominant fish.

5-HT levels

There were no significant differences in 5-HT concentrations between dominant and subordinate fish at any time, nor were there any significant differences between subordinate or dominant individuals and control fish (Fig. 4A–C).

TRP levels

Social interactions appeared to result in a general increase in brain TRP levels in both dominant and subordinate individuals relative to control fish (Fig. 5A–C). After 1 day of

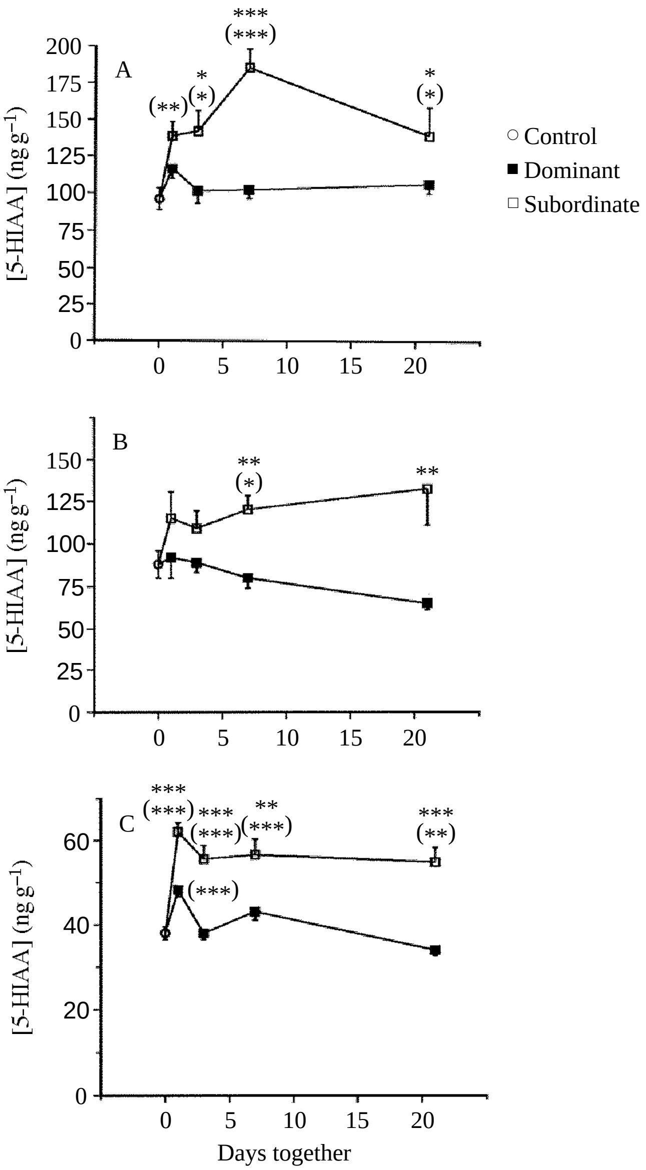

Fig. 2. Concentrations of 5-HIAA in (A) telencephalon, (B) hypothalamus and (C) brain stem of Arctic charr having 1, 3, 7 or 21 days experience of a dominant or subordinate position in a pair. Fish that had been isolated for 1 week were used as controls. Values are means and S.E.M. from 7–10 individuals. Asterisks denote significant differences between dominant and subordinate individuals, whereas asterisks in parentheses denote significant differences from controls. **P*<0.05, ***P*<0.01, ****P*<0.001, Mann–Whitney *U*-test (two-tailed).

pair-rearing, significant increases in TRP concentrations were found in the telencephalon of subordinate fish and in the brain stem of subordinate as well as dominant individuals (Fig. 5A,C). Following longer periods of dominant or subordinate experience, brain TRP levels declined in all three brain parts (Fig. 5A–C). In the brain stem, there were no

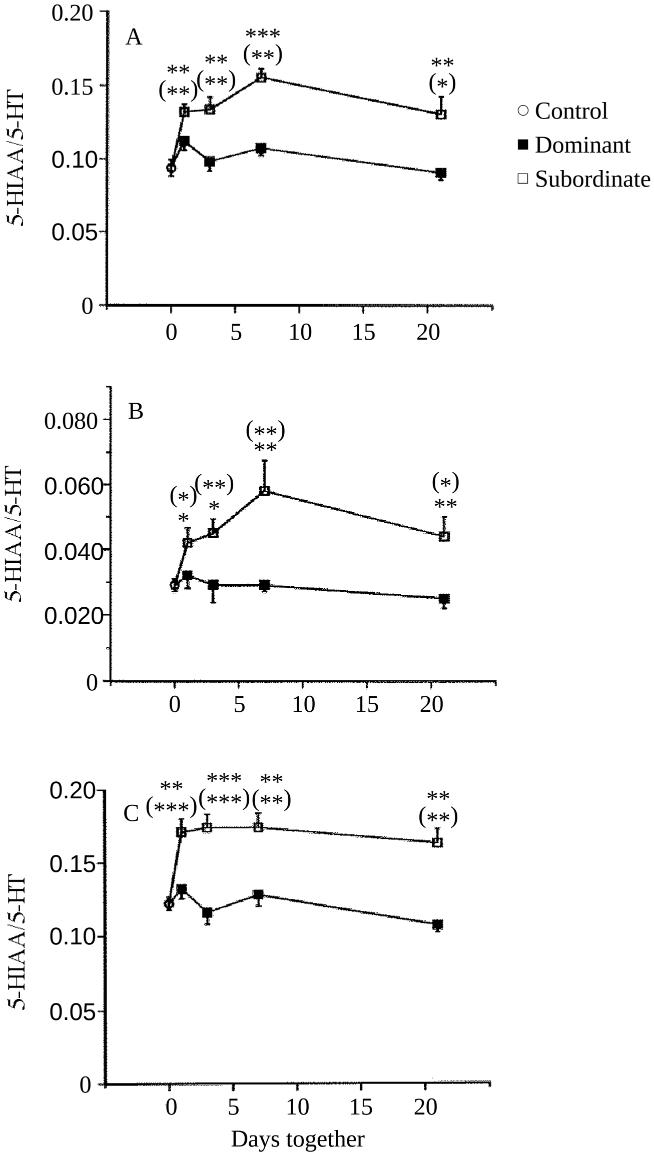

Fig. 3. 5-HIAA/5-HT ratios in (A) telencephalon, (B) hypothalamus and (C) brain stem of Arctic charr having 1, 3, 7 or 21 days experience of a dominant or subordinate position in a pair. Fish that had been isolated for 1 week were used as controls. Values are means and S.E.M. from 7–10 individuals. Asterisks denote significant differences between dominant and subordinate individuals, whereas asterisks in parentheses denote significant differences from controls. *$P<0.05$, **$P<0.01$, ***$P<0.001$, Mann–Whitney *U*-test (two-tailed).

significant differences in TRP concentrations between dominant and subordinate fish at any time (Fig. 5C), but in the telencephalon and hypothalamus, the decreases in TRP levels were more pronounced in subordinate than in dominant individuals (Fig. 5A,B). Thus, subordinate fish had significantly lower TRP concentrations than dominant fish in

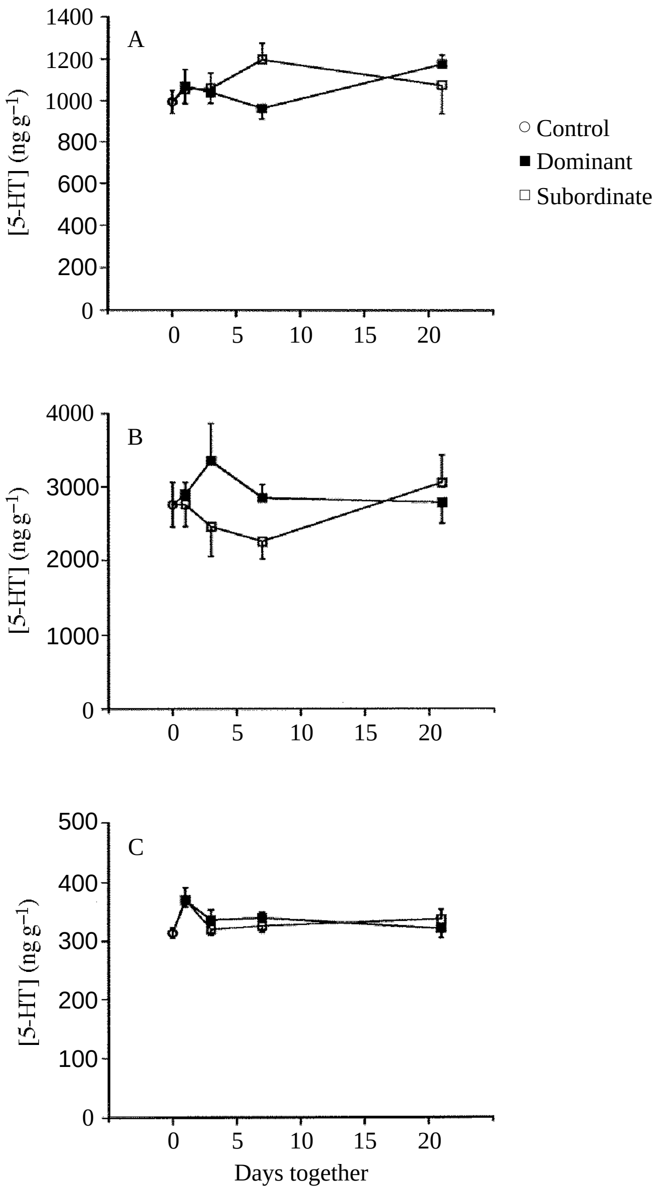

Fig. 4. Concentrations of 5-HT in (A) telencephalon, (B) hypothalamus and (C) brain stem of Arctic charr having 1, 3, 7 or 21 days experience of a dominant or subordinate position in a pair. Fish that had been isolated for 1 week were used as controls. Values are means and S.E.M. from 7–10 individuals.

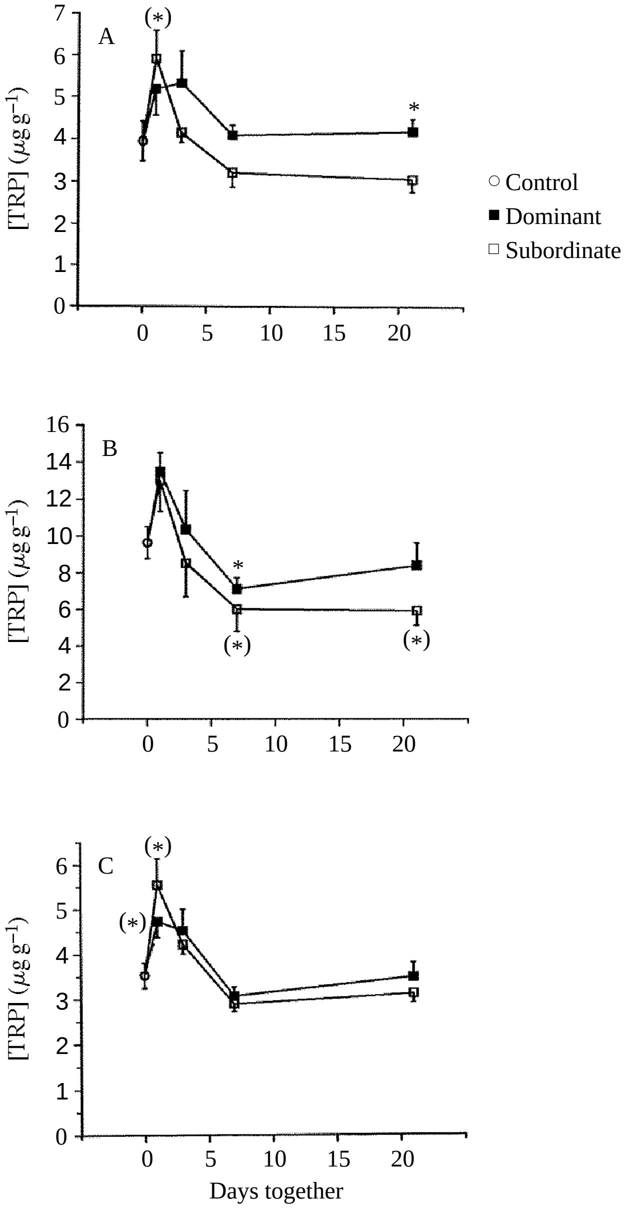

Fig. 5. Concentrations of TRP in (A) telencephalon, (B) hypothalamus and (C) brain stem of Arctic charr having 1, 3, 7 or 21 days experience of a dominant or subordinate position in a pair. Fish that had been isolated for 1 week were used as controls. Values are means and S.E.M. from 4–10 individuals, except for hypothalamus of fish being subordinate for 21 days, where *N*=4. Asterisks denote significant differences between dominant and subordinate individuals whereas asterisks in parentheses denote significant differences from controls. *$P<0.05$, Mann–Whitney *U*-test (two-tailed).

the telencephalon after 21 days (Fig. 5A) and in the hypothalamus after 7 days (Fig. 5C). Furthermore, after 7 and 21 days, subordinate fish had significantly lower TRP concentrations in the hypothalamus than did control fish (Fig. 5B).

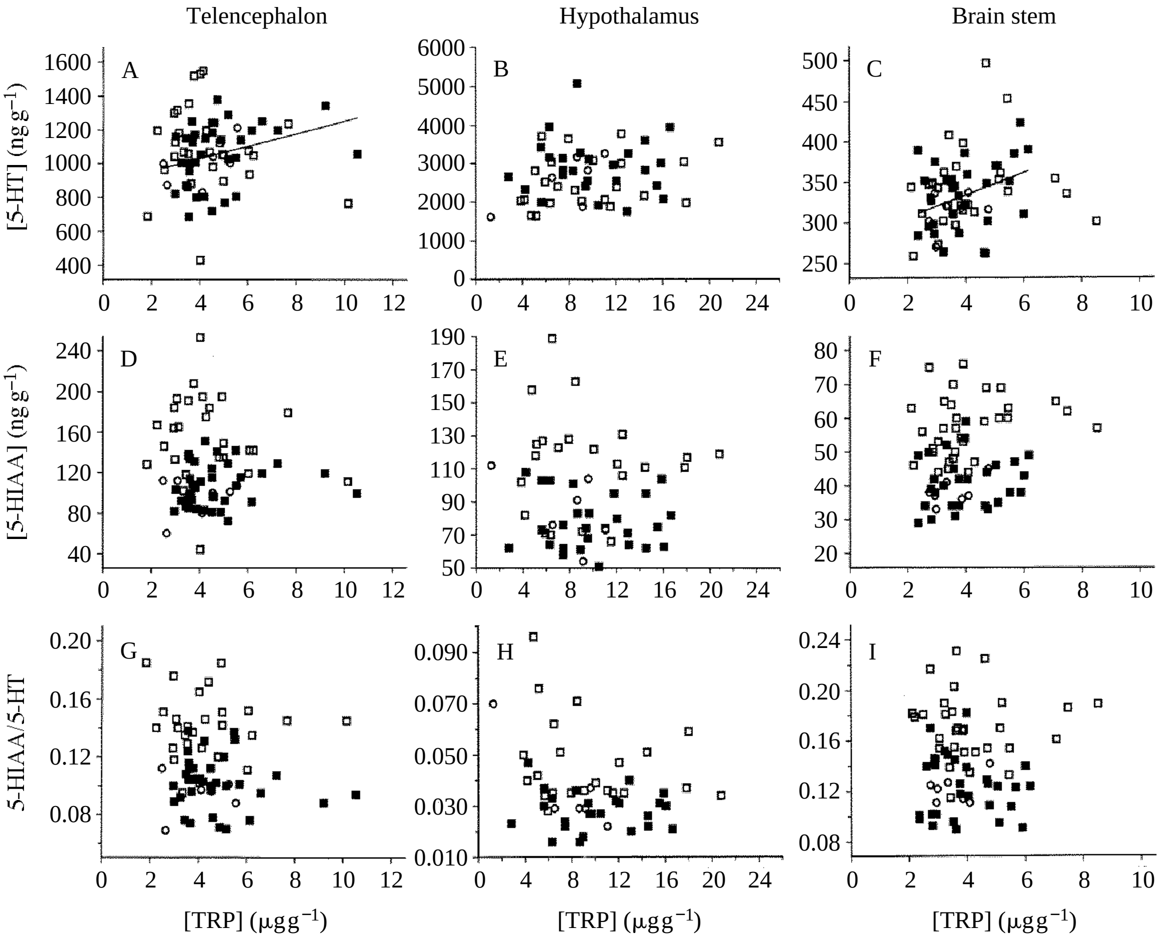

Fig. 6. The relationship between 5-HT concentrations (A–C), 5-HIAA levels (D–F), 5-HIAA/5-HT ratios (G–I) and TRP concentrations in telencephalon (A,D,G), hypothalamus (B,E,H) and brain stem (C,F,I) of Arctic charr having 1–21 days experience of a dominant or subordinate position in a pair. Controls (○) (t=0) were included in the regression lines for dominant (■) as well as for subordinate (□) individuals. Lines are least-square regression lines and correlations were tested using Pearson's correlation coefficient. A, subordinate: r=−0.086, P=0.624; dominant: r=0.334, P=0.033. B, subordinate: r=0.322, P=0.089; dominant: r=0.127, P=0.488. C, subordinate: r=0.182, P=0.267; dominant: r=0.387, P=0.020. D, subordinate: r=−0.046, P=0.791; dominant: r=0.179, P=0.256. E, subordinate: r=−0.035, P=0.856; dominant: r=−0.172, P=0.347. F, subordinate: r=0.286, P=0.077; dominant: r=0.182, P=0.286. G, subordinate: r=0.012, P=0.945; dominant: r=−0.092, P=0.568. H, subordinate: r=−0.287, P=0.132; dominant: r=−0.319, P=0.075. I, subordinate: r=0.125, P=0.447; dominant: r=−0.052, P=0.732.

Correlations between 5-HT, 5-HIAA and 5-HIAA/5-HT ratios and TRP

Significant correlations between 5-HT and TRP concentrations were found in the telencephalon and brain stem of dominant fish (Fig. 6A,C). In contrast, in subordinate individuals no significant correlations were found between TRP levels and 5-HT concentrations in any of the brain parts (Fig. 6A–C). 5-HIAA levels and 5-HIAA/5-HT ratios did not correlate significantly with TRP concentrations in any of the brain parts in dominant or subordinate fish (Fig. 6D–I).

Discussion

The results of the present study show that subordinate experience affects brain serotonin metabolism. Brain 5-HIAA/5-HT ratios were significantly increased in the hypothalamus, telencephalon and brain stem of subordinate Arctic charr following 1 day of exposure to a dominant conspecific. Furthermore, brain 5-HIAA levels and 5-HIAA/5-HT ratios remained high and no decline was seen after 21 days of pair-rearing. The effect of subordinate experience on 5-HT utilization was very similar in different parts of the brain, indicating a wide distribution of these changes.

A key question we have tried to answer in the present experiments was whether the changes seen in 5-HIAA levels and 5-HIAA/5-HT ratios during hierarchic behaviour are the result of altered TRP concentrations in the brain. This was done by studying individual correlations between TRP concentration and 5-HIAA, 5-HT levels and 5-HIAA/5-HT ratios, as well as the time course of changes seen in the brain concentrations of these substances. It should be pointed out that, when mean 5-HT levels remain relatively stable (as in many of the present experiments), the brain 5-HIAA/5-HT ratio is mainly determined by brain 5-HIAA levels. However, 5-HIAA/5-HT ratios provide a more direct index of central serotonergic activity than brain 5-HIAA concentrations *per se*, as variance related to tissue sampling as well as to differences in total levels of 5-HT and 5-HIAA are reduced.

In the present study, social interactions generally resulted in an initial increase in brain TRP concentrations in both subordinate and dominant fish. However, this increase had a short duration and after 3 days of pair-rearing brain TRP levels had returned to control levels. The decline in brain TRP levels was, however, more pronounced in subordinate individuals than in dominants. In contrast, brain 5-HIAA concentrations and 5-HIAA/5-HT ratios remained elevated in subordinate fish even after 21 days of pair-rearing, and no significant correlations were found between either 5-HIAA or 5-HT concentrations and TRP, nor between 5-HIAA/5-HT ratios and TRP, in any of the regions of the brain examined (Fig. 6). Consequently, the prolonged elevation in brain 5-HIAA levels and brain 5-HIAA/5-HT ratios observed in subordinate fish may reflect an increase in 5-HT release and not just a TRP-related increase in intraneuronal 5-HT catabolism. However, the initial short-term increase in brain TRP concentrations may be a mechanism allowing an increase in serotonergic activity without a depletion of 5-HT stores.

Stress has been reported to increase brain TRP concentrations in mammals (Curzon *et al.* 1972; Neckers and Sze, 1975; Dunn, 1988; Dunn and Welch, 1991), but the physiological significance of this increase has been questioned because administration of

TRP seems to increase intraneuronal 5-HT catabolism without affecting 5-HT release (Grahame-Smith, 1971; Lookingland *et al.* 1986; De Simoni *et al.* 1987). However, treatment of rats with valine, an amino acid that competes with TRP for uptake into the brain, has been found to inhibit the stress-induced increase in 5-HT release (Joseph and Kennett, 1983). De Simoni *et al.* (1987) found that TRP administration potentiates the increase in extracellular brain 5-HIAA levels induced by dorsal raphe electrical stimulation in rats, but TRP administration *per se* did not affect extracellular brain levels of 5-HIAA. Thus, the extent to which TRP administration increases functional 5-HT release from serotonergic neurones might depend on the firing frequency of the neurone (Wurtman *et al.* 1981). In mice, 15min of foot shock caused to a decrease in 5-HT levels in the prefrontal cortex and hypothalamus, although both plasma and brain TRP levels increased progressively during the stress treatment (Dunn, 1988). The decrease in 5-HT was reversed after a further 15min of foot shock, leading Dunn (1988) to suggest that the transient decrease in 5-HT reflected a stress-induced increase in 5-HT release that depleted existing 5-HT stores.

Dunn and Welch (1991) argued that the increase in brain TRP concentration during stress could counteract depletion of existing 5-HT stores. However, in the present study the chronic stress caused by a prolonged subordinate experience did not result in any decrease in brain 5-HT levels, in spite of the decrease in brain TRP concentration and the increase in 5-HT flux indicated by the rising 5-HIAA levels. Thus, chronic stress can apparently cause an increased 5-HT synthesis rate although TRP levels are falling. For instance, the activity of tryptophan hydroxylase, the enzyme catalyzing the initial and rate-limiting step in 5-HT synthesis, has been reported to increase in some brain nuclei after chronic stress (Culman *et al.* 1984; Boadle-Biber *et al.* 1989).

The rapid and transient increase in brain TRP levels, observed in both dominant and subordinate fish in the present study, may be indicative of short-term stress in dominant individuals prior to the clear establishment of the dominant–subordinate relationship (Zayan, 1991). An initial brief stress in dominant individuals seemed to be indicated by the increase in brain stem 5-HIAA levels in these fish after 1 day of pair-rearing. Initial stress might have been induced by the removal of the plastic wall that kept the fish separated. However, the fish started to fight within 5–10min of the removal of the partition wall. This makes it unlikely that the removal of the wall was a stressful experience for the fish for more than a few minutes. According to our experience, fish do not fight when frightened (e.g. if they see the experimenter because no nylon-mesh screen is put in front of the aquarium).

Subordinate experience seems to be associated with increased brain serotonergic activity in other vertebrate species, such as talapoin monkeys (Yodyingyuad *et al.* 1985) and rats (Blanchard *et al.* 1991). The fact that socially induced changes in brain serotonergic activity are seen in both mammals and fish suggests that this response is phylogenetically very old and has been conserved during vertebrate evolution. The changes in brain serotonergic activity during social interaction could mediate several of the behavioural characteristics displayed by subordinate fish. For example, brain 5-HT is believed to be involved in the regulation of agonistic behaviour, and in most vertebrates increased serotonergic activity appears to have an inhibitory effect on aggressive behaviour (Avis, 1974; Huntingford and Turner, 1987; Miczek *et al.* 1989). Indeed, intracranial injections of 5-HT have been found to reduce aggressive behaviour in fish (Munro, 1986; Maler and Ellis, 1987).

The brain serotonergic system is also believed to be involved in the regulation of feeding behaviour and increased serotonergic activity has been found to have an inhibitory effect on feeding in mammals (Fernstrom, 1981; Samanin, 1989). We have previously shown that growth rate is positively correlated with social rank in Arctic charr (Winberg *et al.* 1992*a*), and this was also evident in the present study, where subordinate individuals lost weight. This could be explained by the fact that subordinate individuals had reduced access to food since feeding attempts by subordinates often induced attacks from the dominant fish, but Abbott *et al.* (1985) reported that subordinate fish reduced feeding voluntarily.

Furthermore, the central serotonergic system is thought to be involved in the regulation of spontaneous locomotor activity in mammals (Gerson and Baldessarini, 1980) and a similar role has been indicated in fish (Fenwick, 1970; Fingerman, 1976). In both the present study and previous studies on Arctic charr (Winberg *et al.* 1991, 1992*a*), subordinate fish showed reduced locomotor activity compared with dominants, and artificially stressed Arctic charr display a reduction in motor activity as well as increased 5-HIAA/5-HT ratios (Winberg *et al.* 1992*b*). Thus, the decreased locomotor activity observed in subordinate fish could, at least partly, be an effect of the increased serotonergic activity.

Finally, it has been suggested that increased serotonergic activity may decrease behavioural responsivity (Geyer *et al.* 1976) and it is tempting to suggest that the behavioural effects mentioned above reflect such a modulatory effect of 5-HT, allowing the subordinate fish to cope with the chronic stress imposed by the presence of the dominant individual.

In conclusion, the results of the present study show that subordinate experience has a rapid and dramatic effect on 5-HT metabolism which is not directly related to a concomitant increase in brain TRP levels. Thus, the increases in brain 5-HIAA concentration and brain 5-HIAA/5-HT ratios displayed by subordinate Arctic charr are likely to reflect an increase in the activity of the 5-HT neurotransmitter systems.

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