THE EFFECTS OF SEROTONIN AND 5-CARBOXAMIDOTRYPTAMINE ON AGGRESSIVE BEHAVIOR IN CRAYFISH PAIR INTERACTIONS

LISA MANGIAMELE

Introduction

Agonistic interactions between decapod crustaceans consist of a series of bouts characterized by combative use of the claws to strike, grasp, and restrain the opponent. The antennae may also be used as weapons to tap or whip the body of another individual. Fights that escalate in intensity often involve one animal pulling or lifting its opponent above the substrate, and those battles that reach the highest level of intensity may result in individuals attempting to violently break off the appendages of the opponent. These aggressive behaviors are highly stereotyped, and usually interactions result in a clear winner and loser (Bruski and Dunham 1987; Huber and Kravitz 1995). Changes in behavior during these interactions, where winning appears to reinforce aggressive behavior while losing appears to inhibit aggression, aid in the formation of a dominance hierarchy (Issa et al 1999).

The neurohormone serotonin [5-hydroxytryptamine (5HT)] has been linked to agonistic behavior and aggressive posturing in lobsters and crayfish (Livingstone et al. 1980; Antonsen and Paul 1997; Huber et al. 1997). Crayfish treated with 5HT show increased intensity of aggressive response to conspecifics, and are more likely to continue fighting in situations that would normally evoke a retreat (Huber et al. 1997). The similarity of this response to the increased aggression exhibited by dominant animals suggests a role for endogenous serotonin in fighting behavior and the maintenance of social status. In addition, amine injection has been found to elicit characteristic postures in the absence of external stimuli. Injections of 5HT in isolated crayfish and lobsters have been shown to produce the high stance, curled tail, and raised chelae that has traditionally been interpreted as an "aggressive" posture (Livingstone et al. 1980; Antonsen and Paul 1997).

The neural mechanisms of aggression and social dominance are still unknown. However, it is believed that serotonin may act in both the central nervous system and periphery to influence motor programs controlling the threat postures and escape mechanisms that characterize agonistic encounters. Serotonin has been found to alter the excitability of motorneurons responsible for postural flexion and extension (Harris-Warrick and Kravitz 1984). It can also directly affect abdominal extensors by increasing the intensity of electrically stimulated muscle contractions (Harris-Warrick and Kravitz 1984). In addition, the command neuron controlling tail flips, the lateral giant (LG), is known to be modulated by 5HT (Yeh et al. 1997). The effect of serotonin on the LG neuron has been found to change in response to the social experiences of dominance or subordinance. Application of exogenous serotonin inhibited the response of the LG neuron in social subordinates, a neuronal change that would most likely contribute to a decreased incidence of escape behavior and an increased likelihood to engage in combat (Yeh et al. 1997).

In this experiment, I tested the behavioral effects of 5-hydroxytryptamine (5HT) and 5-carboxamidotryptamine (5CT), a $5HT_{1A}$ receptor agonist, on pairs of interacting crayfish (`Procambarus clarkii`). 5CT has been frequently used in vertebrates as a potent agonist for non-selective activation of $5HT_1$ receptors (Wedderburn and Sillar 1994; Villalon et al. 1997). In my study, 5CT was used to elucidate the role of serotonin receptor activation on neural circuits involved in agonistic behaviors. I collected data on aggressive and submissive behaviors that occur during agonistic competitions between two unfamiliar crayfish, and compared drug groups for significant differences in the frequency of aggressive acts. Based on previous experiments, it was expected that both serotonin and 5CT would increase aggressive displays and postures. My results show that 5CT significantly increases aggressive posture during interactions. In contrast to previous reports, 5HT did not increase aggressive behavior.

An additional aim of this study was to compare the results of behavioral analysis performed 5 minutes post-injection and 30 minutes post-injection. Edward Kravitz believes that it takes 30 minutes for 5HT injections to take effect and significantly increase aggressive behavior (personal communication with Dr.Tierney). In this study, I provide evidence to refute this claim, and show that 5HT does not enhance aggressiveness in 5 or 30 minutes post-injection trials.

Materials and Methods

Adult male crayfish (Procambarus clarkii) were obtained from a commercial supplier and housed in community tanks (50 X 50 X 25 cm) supplied with flowing spring water at 13-14^{o} C . They were fed Purina Trout Chow. Healthy and intact adult male crayfish weighing between 17.2 – 42.0 grams (average of 23.4 grams) were selected from the population and placed in small isolation aquaria (30 X 15 X 20 cm) filled with cold spring water. Animals were allowed to acclimate for approximately 48 hours before injection. Crayfish were grouped in size-matched pairs (less than 2 g difference), and white markings were used to distinguish between animals in a pair. Pairs of crayfish were randomly assigned to one of three groups (5HT, 5CT, or control) with an even distribution of sizes in each group.

Trial 1 – Begun 5 minutes post-injection

Solutions of 5CT and 5HT were prepared at concentrations of 5×10^{-4} M in cold crayfish saline. A pair was randomly selected for testing, and each animal was given an identical 100 µL injection of 5CT, 5HT, or saline. Crayfish were placed on opposing sides of a small aquarium (30 X 15 X 20 cm) with a flat gravel bottom, separated by an opaque divider, and allowed to acclimate for approximately 5 minutes. After acclimation, the divider was removed and behavior was videotaped for 20 minutes.

Trial 2 – Begun 30 minutes post-injection

After completion of the first trial the investigator broke off any agonistic encounters, and the divider was again put in place to separate crayfish in opposite sides of the tank. After 10 minutes had passed (approximately 30 minutes after the original injection), the divider was removed and behavior was videotaped for 20 minutes.

Data Analysis

Subsequent analysis of videotapes was performed by a trained observer (the author). To maintain objectivity, the identity of the substance injected was unknown at the time of data analysis. I recorded the length of time each crayfish spent exhibiting the following stereotyped behaviors: chelae contact, body up, antenna wave, antenna up. Also recorded was the number of times each animal performed the following acts: approach (within one body length), lunge, meral spread, chela grasp, retreat, tail flip, and antenna tap. By my definition, an approach is the movement of one animal toward the other, not always leading to contact, but usually evoking a response (i.e., retreat, tail flip). A lunge is distinguished as a very rapid approach, or one animal charging toward the other. A retreat is defined as the movement of one animal away from an approaching animal, or one animal breaking contact and moving off to a distance of more than one body length. For the purpose of discussion and comparison, I classified the following behaviors as aggressive: chelae contact, body up, antenna up, approach, lunge, meral spread, chela grasp, and antenna tap. Submissive behaviors included retreats and tail flips and antenna wave.

Statistical Tests

The data was analyzed using SPSS version 10.0 for Windows. Non-parametric statistical methods were used, as behavioral data sometimes produced extreme outliers and did not represent a normal distribution. A Kruskal-Wallis test was used to determine overall significance. If significant difference between groups was detected by the Kruskal-Wallis, a Mann-Whitney U test was to further elucidate significant differences between two independent groups.

Results

A Kruskal-Wallis test was applied to the behavioral data (n = 11 for 5HT and 5CT, n=12 for control) relating the drug administered to the frequency or duration of each agonistic behavior. Results were significant ($p \leq 0.05$) for six behaviors in Trial 1: approach, lunge, retreat, contact, body up, and antenna up (Table 1).

Kruskal-Wallis Test (df=2)

	Mean	Std. Error $\pm$	P
Approach	5CT[1] 8.9091 5HT[2] 2.3636 Cont[3] 10.8333	0.9578 0.5270 1.9181	.000
Lunge	5CT 0.9091 5HT 0.09091 Cont 0.9167	0.3149 0.09091 0.3580	.050
Spread	5CT 1.9091 5HT 0.4545 Cont 2.1667	0.7441 0.2073 0.7265	.129
Grasp	5CT 6.5455 5HT 2.9091 Cont 3.3333	1.9880 1.3847 1.0249	.198
Antenna Tap	5CT 5.8182 5HT 1.0909 Cont 2.0833	2.1651 0.8362 0.6793	.132
Retreat	5CT 6.4545 5HT 2.0000 Cont 7.9167	1.1470 0.6467 1.0110	.001
Tail Flip	5CT 4.2727 5HT 1.0000 Cont 5.2500	1.2438 0.5222 1.6566	.060
Contact (in seconds)	5CT 305.0909 5HT 156.3409 Cont 196.5400	47.3751 64.2575 29.4801	.035
Body Up (in seconds)	5CT 685.0636 5HT 399.3673 Cont 384.1103	63.6899 74.5636 29.4817	.003
AntennaWave (in seconds)	5CT 42.3345 5HT 23.0500 Cont 24.6825	16.8508 12.1316 11.6263	.624
Antenna Up (in seconds)	5CT 552.7782 5HT 194.1800 Cont 345.3908	68.1976 46.1857 36.8133	.000

[1] n=11
[2] n=11
[3] n=12

Table 1. Trial One – 5 minutes post-injection. Differences between drug groups in behaviors recorded during agonistic interactions between pairs of crayfish 5 minutes post-injection. Significant comparisons ($p \leq 0.05$) are from Kruskal-Wallis one-way ANOVA across groups. 5CT = 5-carboxamidotryptamine; 5HT = 5-hydroxytryptamine; Cont = control saline injection.

To further determine the origin of significant differences between groups, several Mann-Whitney U tests were performed. These yielded significant results for 5HT in decreased approach, retreat, and antenna up when compared to control (Table 2), as well as significant results for 5CT in increased body up and antenna up over control (Table 3).

	Approach	**Retreat**	**Antennae Up** (in seconds)
p	.000	.001	.011

Table 2. Mann-Whitney U Test – 5HT vs. Control.
Significant differences ($p \leq 0.05$) between 5HT and saline groups recorded during agonistic interactions between pairs of crayfish 5 minutes post-injection.

	Body Up (in seconds)	**Antennae Up** (in seconds)
p	.000	.023

Table 3. Mann-Whitney U Test – 5CT vs. Control.
Significant differences ($p \leq 0.05$) between 5CT and saline groups recorded during agonistic interactions between pairs of crayfish 5 minutes post-injection.

The majority of significant difference between groups occurred between 5HT and 5CT in the areas of approach, retreat, tail flip, contact, body up, and antenna up (Table 4). Animals treated with 5HT showed a decreased likelihood of exhibiting each behavior.

	Approach	**Retreat**	**Tailflip**	**Contact** (in seconds)	**Body Up** (in seconds)	**Antennae Up** (in seconds)
p	.000	.001	.028	.019	.028	.000

In contrast, for Trial 2, no significant difference was found in the frequency or duration of agonistic behaviors in response to either 5CT or 5HT (Table 5). Therefore, we can conclude that behavioral responses after 30 minutes post-injection are not significantly more aggressive than control, and that any behavioral effects caused by exogenous 5HT or 5CT can only be seen within a 5-30 minute period after injection.

	Mean	Std. Error ±	P
Approach	5CT[1] 8.8333 5HT[2] 5.5000 Cont[3] 8.6000	2.1972 1.4318 3.0304	.533
Lunge	5CT 1.3333 5HT 0.8333 Cont 0.5000	0.4944 0.4014 0.3416	.401
Spread	5CT 0.6667 5HT 0.6667 Cont 0.3333	0.2108 0.3333 0.2108	.557
Grasp	5CT 0.8333 5HT 1.3333 Cont 1.1667	0.1667 0.9888 0.4773	.741
Antenna Tap	5CT 0.0000 5HT 0.0000 Cont 1.3333	0.0000 0.0000 0.8433	.119
Retreat	5CT 7.8333 5HT 5.0000 Cont 6.5000	1.7780 1.2383 1.6882	.397
Tail Flip	5CT 4.5000 5HT 2.1667 Cont 2.3333	1.9621 0.8724 1.5846	.335
Contact (in seconds)	5CT 122.3733 5HT 73.0017 Cont 141.0083	36.7304 25.7710 44.0185	.372
Body Up (in seconds)	5CT 467.6267 5HT 431.5917 Cont 339.3367	75.5708 64.5420 88.5045	.581
AntennaWave (in seconds)	5CT 5.0450 5HT 8.9800 Cont 6.8617	3.3209 4.0263 2.7707	.771
Antenna Up (in seconds)	5CT 360.4783 5HT 267.0467 Cont 299.4833	58.5134 49.8123 86.3965	.653

Table 5. Trial Two – 30 minutes post-injection.
Differences between drug groups in behaviors recorded during agonistic interactions between pairs of crayfish 30 minutes post-injection. Significant comparisons ($p \leq 0.05$) are from Kruskal-Wallis one-way ANOVA across groups. 5CT = 5-carboxamidotryptamine; 5HT = 5-hydroxytryptamine; Cont = control saline injection.

Effects of 5HT on posture and behavior

5HT did not produce an increase in aggressive behaviors or posture (Table 2). In fact, animals that received 5HT were less aggressive than controls in two important areas. 5HT treated animals (n=11;

m=194.18 ± 46.1857) spent significantly less time than controls (n=12; m=345.3908 ± 36.8133) (p=0.011) exhibiting the antennae up behavior that often characterizes agonistic encounters. 5HT animals (n=11; m=2.3636 ± 0.5270) were also less likely to approach an opponent than controls (n=12; m=10.8333 ± 1.9181)(p=0.000), showing a possible decreased willingness to fight. Additionally, it was found that animals injected with 5HT (n=11; m=2.0000 ± 0.6467) were less likely than controls (n=12; m=7.9167 ± 1.0110)(p=0.001) to retreat from an encounter.

Effects of 5CT on posture and behavior

Injections of 5CT appeared to induce aggressive postures and displays in crayfish (Table 3). Animals treated with 5CT (n=11; m=685.0636 ± 63.6899) spent more time in the body up posture than controls (n=12; m=384.1103 ± 29.4817)(p=.000). In addition, 5CT animals (n=11; m=552.7782 ± 68.1976) exhibited antenna up behavior more often than controls (n=12; m=345.3908 ± 36.8133)(p=0.023).

Comparison of 5HT and 5CT

5CT appears to increase aggressive displays, while 5HT decreased the expression of aggressive behavior and posture. The incidence of several behaviors was significantly lower in animals treated with 5HT than those given 5CT. 5CT animals (n=11; m=8.9091 ± 0.9578) approached their opponent more often than did 5HT animals (n=11; m=2.3636 ± 0.5270)(p=0.000). 5CT animals also exhibited body up posture (n=11; m=685.0636 ± 63.6899)(p=0.028) and displayed antenna up (n=11; m=552.7782 ± 68.1976)(p=0.000) more often than those injected with 5HT. They were also in contact with their opponent (n=11; m=305.0909 ± 47.3751) for longer periods of time than those animals treated with 5HT(n=11; m=156.3409 ± 64.2575)(p=0.019), thus further supporting the conclusion that 5HT does not increase aggressiveness in this experiment.

In addition, the incidence of escape behavior in 5HT animals was less frequent than in 5CT animals. 5HT animals (n=11; m=2.0000 ± 0.6467) showed a lowered tendency to retreat from their opponent than did 5CT animals (n=11; m=6.4545 ± 1.1470)(p=0.001). Crayfish that were injected with 5HT (n=11; m=1.0000 ± 0.5222) also performed less tail flips than did those injected with 5CT (n=11; m=4.2727 ± 4.1253)(p=0.028).

Discussion

The main goal of this study was to quantify the behavioral response of crayfish to serotonin and 5CT, a $5HT_1$ receptor agonist, and to shed some light on the possibility that serotonin might play a role in aggression and the maintenance of social dominance. My results show a considerable difference in behavioral response to 5HT and 5CT (Table 4). Contrary to previous reports (Livingstone et al. 1980; Antonsen and Paul 1997; Huber et al. 1997), I found that exogenous 5HT did not increase aggressiveness. Instead, 5HT caused a decrease in aggressive displays when compared with control animals (Table 2). I found that crayfish injected with 5HT were less likely to approach their opponent for combat (Fig.1, Table 2), and exhibited less of the antenna up threat display (Fig. 4, Table 2). These results coincide with the observations of Peeke et al. (2000), who showed that animals treated with high doses (3.0 mg/kg) of 5HT impaired their ability to win agonistic encounters against opponents that were treated with saline. Peeke et al. (2000) suggested that the apparent lack of aggression shown by animals injected with 5HT could be attributed to an overall slowing of locomotor activity.

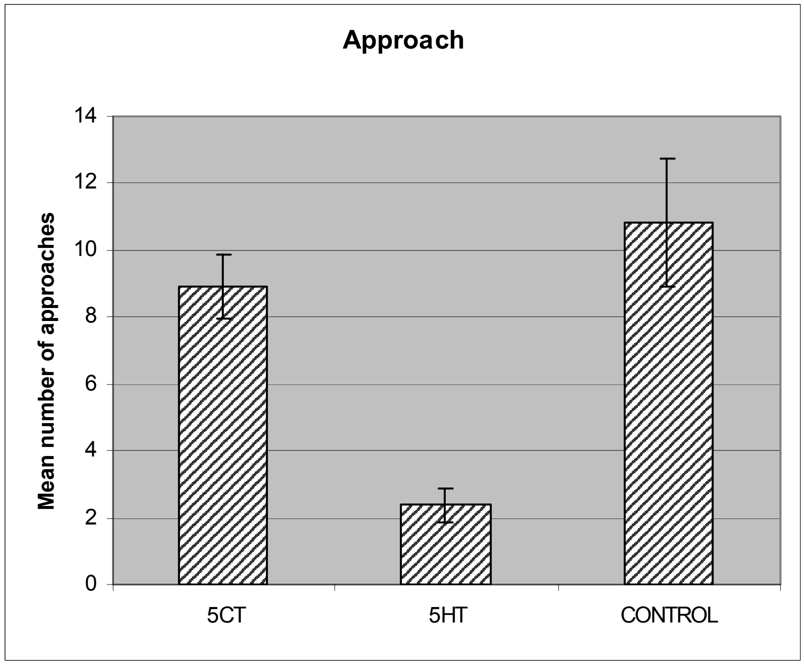

Figure 1. Approaches performed by crayfish during agonistic interactions between pairs of individuals 5 minutes post-injection. Data represent the mean (± SE) number of times the behavior was performed during 20-minute observation periods.

In this study, the observer's qualitative observations show several incidences of instability and lethargy in one or both animals of a pair injected with 5HT. In addition, two pairs injected with 5HT did not come into contact at all during the 20-minute taping period, but instead remained relatively motionless in their respective corners. It is also possible that some animals administered exogenous 5HT have an adverse reaction to the substance, thus contributing to malaise or a general lack of motivation to engage the opponent. Although crayfish in this experiment did not seem to be extremely adversely affected by 5HT, previous posture experiments I performed showed that several 5HT animals were incapacitated by the injection and assumed a legs-bent, tail-curled posture that was not reminiscent of the high aggressive stance normally taken by crayfish in agonistic encounters (unpublished observations). This effect suggests that 5HT may be acting in some way to diminish aggressive posture and behavior in these experiments.

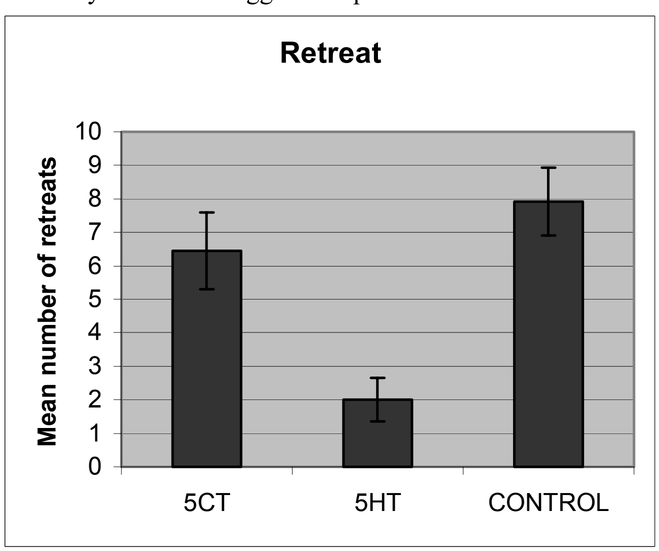

Figure 2. Retreats performed by crayfish during agonistic interactions between pairs of individuals 5 minutes post-injection. Data represent the mean (± SE) number of times the behavior was performed during 20-minute observation periods.

Huber et al. (1997) have suggested that serotonin increases aggressiveness in crayfish by decreasing motivation to retreat. They found that injection of 5HT into a subordinate animal caused it to engage in fights for longer periods of time; thus, 5HT apparently increased the animal's interest in fighting (Huber et al. 1997). In this study, I also found that crayfish injected with 5HT were less likely to retreat from an encounter than control animals (Fig. 2, Table 2). However, the relatively mild and intermittent nature of the encounters did not lead me to conclude that this finding was evidence of an increased aggressive motivation. I did not find a significant increase over controls in chelae contact between animals treated with 5HT (Table 1). On the contrary, fighting was sporadic and usually involved slow approaches and brief contact between individuals, so that retreats were not necessary to break off the encounter. In addition, decreased incidence of retreat in animals treated with 5HT may simply reflect an overall reduction in movement caused by exogenous 5HT. Yeh et al. (1997) found that serotonin inhibited the firing of the LG neuron, which controls tail flip behavior. When approached, 5HT treated crayfish may not have the ability to tail flip, or may simply move just far enough away to avoid physical contact with the opponent. In short, animals treated with 5HT may have a delayed response to attack and may be less likely to retreat, thus contributing to the decreased frequency of retreat found in this study.

The results of this study suggest a role for the activation of $5HT_1$ receptors in the enhancement of aggressive postures and certain threat displays in crayfish, although the possible involvement of other subtypes cannot be ruled out. The failure of exogenous 5HT to increase aggression in this experiment suggest that a complex mechanism of 5HT receptor activation, perhaps acting in combination with other monoamines (e.g., dopamine, octopamine), may be involved in mediating agonistic behavior. In this experiment, I found that 5CT increased the amount of time crayfish spent in the body up and antenna up position (Fig. 3, Fig. 4, Table 3).

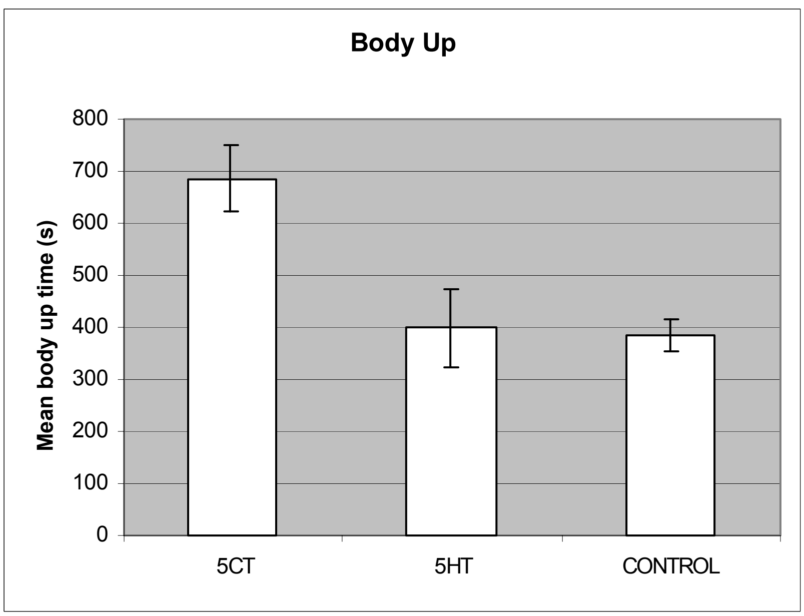

Figure 3. Amount of time crayfish spent in body up posture during agonistic interactions between pairs of individuals 5 minutes post-injection. Data represent the mean (± SE) amount of time pairs performed this behavior during 20-minute observation periods.

During agonistic encounters between crustaceans, the body is held high off the substrate, the tail is lifted up in a U shape, and the antennae are kept rigid and positioned up and away from the chelae of the opponent. This posture makes the crayfish look larger and more threatening, and may function both as a defense behavior and an aggressive display (Tierney et al. 2000). In our study, crayfish treated with 5CT walked high with legs straightened and body elevated approximately 2-3 cm above the substrate. Antennae were frequently held perpendicular to the body, and chelae were open and slightly raised. Although the aggressive posture exhibited by animals treated with 5CT did not exactly mimic the body positioning of crayfish in combat, the rigid and alert stance seen was in sharp contrast to the low, relaxed posture that 5HT animals displayed in this experiment. A crayfish assuming the 5CT posture seen in this study would signal an agitated state to a conspecific, and thus act to prepare the opponent for an agonistic bout. Therefore, we can suggest that the posture induced by 5CT in this study was an aggressive display.

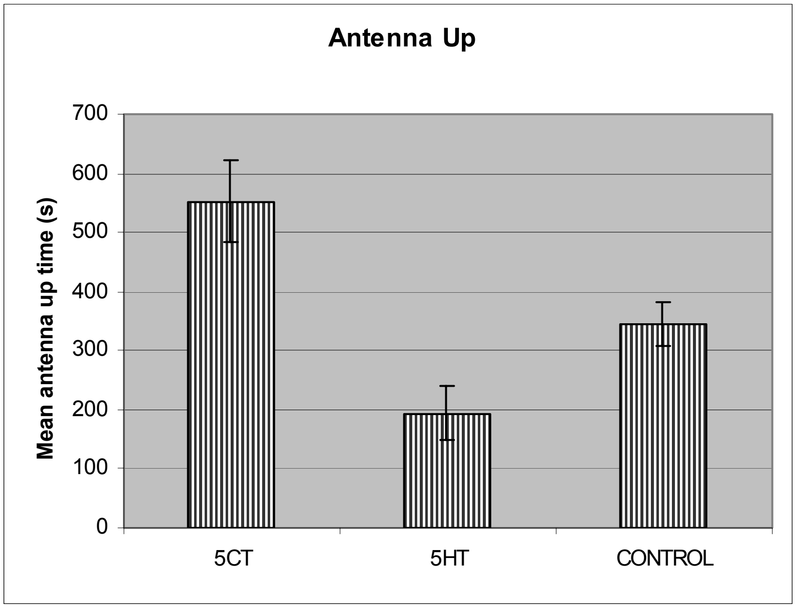

Figure 4. Amount of time crayfish spent in antenna up posture during agonistic interactions between pairs of individuals 5 minutes post-injection. Data represent the mean (± SE) amount of time pairs performed this behavior during 20-minute observation periods.

In addition, it was noted that the intensity of encounters between pairs injected with 5CT was in some cases elevated above that of 5HT or control pairs. Observer notes indicate three separate incidences of one crayfish in a pair grasping the opponent and tossing it on its back. Such violent behavior was not common of agonistic encounters in this experiment. Fights between crayfish will normally escalate in intensity the longer they last (Huber and Kravitz 1995); however, in this experiment bouts between pairs treated with 5CT did not last significantly longer than controls (Table 1). In light of this fact, a higher level of intensity in a short period of contact could be considered an indicator of an enhanced aggressive state influenced by 5CT.

A second aim of this study was to ascertain the time required for injections to significantly affect aggressive behavior. It has been suggested by Kravitz that the aggression enhancing effects of serotonin injections cannot be seen until 30 minutes post-injection (personal communication). However, other reports suggest the contrary. Huber et al. (1997) report that the fight-enhancing effects of 5HT on crayfish were attenuated by 30 minutes post-infusion. Furthermore, Peeke et al. (2000) show that levels of 5HT in the hemolymph of juvenile lobsters are high immediately following injection, and remain high throughout the 30 minutes post-injection, though there is a large drop in circulating 5HT after 5 minutes. My results also refute Kravitz' statement in showing no significant differences in aggressive behavior when encounters were taped 30 minutes post-injection (Table 5). In contrast, I found several significant changes in behavior in response to 5HT and 5CT when crayfish were observed just 5 minutes post-injection (Tables 2 & 3).

In conclusion, this study offers several interesting insights into the study of the neurochemical basis of crustacean aggression. These results show a considerable difference in the behavioral effects of exogenous 5HT and 5CT, a potent $5HT_1$ receptor agonist. In contrast to available literature, I provide evidence that exogenous serotonin does not increase aggressive behavior in this experiment, but instead appears to inhibit aggressive posture and motivation, possibly due to an overall decrease in motor activity. I also found that 5CT appears to enhance aggressive posture and, in some cases, cause a quicker escalation of fight intensity in a short period of time. In addition, I provide evidence that the behavioral effects of 5HT and 5CT can be seen within 30 minutes post-injection. These findings could potentially contribute a small step toward elucidating the role of serotonin in modulating the neural mechanisms of aggressive behavior in invertebrates.

REFERENCES CITED

Antonsen, B.L. and Paul, D.H. (1997). Serotonin and octopamine elicit stereotypical agonistic behaviors in the squat lobster Munida quadrispina. Journal of Comparative Physiology A 181: 501-510.

Bruski, C.A. and Dunham, D.W. (1987). The importance of vision in agonistic communication of the crayfish Orconectes rusticus. An analysis of bout dynamics. Behavior 103: 87-107.

Harris-Warrick, R.M. and Kravitz, E.A. (1984). Cellular mechanisms for modulation of posture by octopamine and serotonin in the lobster. Journal of Neuroscience 4(8):1976-1993.

Huber, R. and Kravitz, E.A. (1995). A quantitative analysis of agonistic behavior in juvenile American lobsters (Homarus americanus). Brain, Behavior, and Evolution. 46: 72-83.

Huber, R., Smith, K., Delago, A., Isaksson, K., and Kravitz, E.A. (1997). Serotonin and aggressive motivation in crustaceans: Altering the decision to retreat. Proceedings of the National Academy of Science USA 94: 5939-5942.

Issa, F.A., Adamson, D.J., and Edwards, D.H. (1999). Dominance hierarchy formation in juvenile crayfish Procambarus clarkii. Journal of Experimental Biology 202: 3497-3506.

Livingstone, M.S., Harris-Warrick, R.M., Kravitz, E.A. (1980). Serotonin and octopamine produce opposite postures in lobsters. Science 208: 76-79.

Tierney, A.J., Godleski, M.S., and Massanari, J.R. (2000). Comparative analysis of agonistic behavior in four crayfish species. Journal of Crustacean Biology 20(1): 54-66.

Villalon, C.M., Contreras, J., Ramirez-San Juan, E., Castillo, C., Pusquia, M., Terron, J.A. (1995) Characterization of prejunctional 5HT receptors mediating inhibition of sympathetic vasopressor responses in the pithed rat. British Journal of Pharmacology 116(8):3330-6

Wedderburn, J.F. and Sillar, K.T. (1994). Modulation of rhythmic swimming activity in post-embryonic Xenopus laevis tadpoles by 5-hydroxytrypatmine acting at 5HT1A receptors. Proceedings of the Royal Society of London Biological Sciences 257(1348): 59-66.

Yeh, S., Musolf, B.E., and Edwards, D.H. (1997). Neuronal adaptations to changes in the social dominance status of crayfish. Journal of Neuroscience 17(2):697-708.