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Oral L-Dopa Disrupts Behavioral Self-Control in Male Fighting Fish (*Betta splendens*)

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Abstract

In their natural habitat, male *Betta splendens* are territorial resource defenders, whereas females are non-territorial opportunistic foragers. This ecological difference suggests that males may be more capable of delaying gratification for food rewards. The present study examined impulsive choice in *Betta splendens* through two experiments comparing subjects' choices between a Smaller-Sooner (SS) reward (1 pellet immediately) and a Larger-Later (LL) reward (3 pellets after 15 s). In Experiment I, the choice distributions of males were more likely to stabilize on the LL option over the SS option, whereas females' choice distributions were equally likely to stabilize on either option. These findings indicate that most males demonstrated spontaneous behavioral self-control without specialized training, while females were collectively indifferent. Experiment II investigated whether dopamine modulates this behavior by administering oral L-Dopa (60 mg/kg) to males before trials. Using the same procedures, only 30% of L-Dopa-treated males' choice distributions stabilized on the LL reward, while 70% of experimental males' choice distributions stabilized on the SS option; the choice distributions of control males were equally likely to stabilize on either reward. These results suggest that elevated dopaminergic activity increases impulsive choice in male *Betta splendens*. Future studies should examine dopamine agonists and antagonists, as well as female responses, to further clarify dopamine's role in reward valuation and behavioral self-control in *Betta splendens*.

Keywords: *Betta splendens*; behavioral self-control; impulsive choice; dopamine; L-dopa; reward valuation

Key Contribution: This study demonstrates that domesticated male *Betta splendens* exhibit behavioral self-control by choosing larger, delayed food rewards, and this capacity can be disrupted by oral L-Dopa administration. These findings establish domesticated *Betta splendens* as a promising model for studying the evolutionarily conserved dopaminergic mechanisms underlying impulsiveness and reward-based decision-making.

1. Introduction

Behavioral impulsiveness can be defined as the choice of smaller and more immediately available rewards over larger, but delayed, rewards, while behavioral self-control is the choice of the latter over the former [1–4]. The ability to delay the gratification of obtaining a smaller reward and waiting to acquire a larger, but delayed reward, i.e., behavioral self-control, has been displayed to varying degrees across a remarkable number of both mammalian and non-mammalian species [1,2,5–10]. This behavioral capacity even extends to invertebrates, such as honeybees (*Apis mellifera*; 11,12) and cuttlefish (*Sepia officinalis*; 13). Traditionally, behavioral impulsiveness and self-control have been experimentally investigated using primary food rewards obtained via either two-key operant choice tasks or instrumental discrete-trial choice tasks [5,7,11,13–15]. It is important to note a subtle distinction between these two techniques. Subjects tested under two-key operant choice procedures must respond to satisfy a particular reinforcement contingency in order to be presented with the

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reward (typically in operant-response chambers under concurrent reinforcement schedules). Similarly (but not identically), subjects tested under instrumental discrete-trial choice procedures must respond in such a way as to physically move into a location where the reward is presented (typically inside a type of maze). More recently, a stable choice for larger yet delayed rewards was demonstrated in African gray parrots (*Psittacus erithacus*) that received tokens as a secondary reward, as opposed to a primary food reward [16] (for an earlier review of token economies, see [17]). Taken together, these results indicate that the capacity for behavioral self-control extends beyond mammalian species and is likely the result of behavioral adaptations under various selection pressures.

A species' capacity for behavioral self-control may be determined by natural history and evolved behavioral capacities [13,18]. Animals that rely on transient prey, such as the common cuttlefish (*Sepia officinalis*), display behavioral self-control in a delay maintenance task [13]. Similarly, cleanerfish (*Labridae dimidiatus*) will routinely ignore smaller fish that present less mucus and wait for larger fish that present a larger amount of mucus for the cleaner fish to feed upon; cleaner fish thus rival primates on quantitative delayed gratification tasks [18]. The preceding examples fit within a larger framework under the *Life History Hypothesis* [19] (for a recent review, see [20]), which posits that organisms must balance tradeoffs among growth, maintenance, and reproduction. For a territorial male *Betta splendens*, one manner in which these tradeoffs are manifested is found in a males' choices between defending territory from potential rivals versus courting potentially receptive females that enter their territory [21–23]. To navigate these tradeoffs successfully, some response patterns (e.g., aggression and territorial defense) must be inhibited. In contrast, other response patterns (e.g., courtship and mating) are activated when a female approaches, while an opposite pattern emerges when a rival male approaches [21,24]. Thus, the life history hypothesis predicts that territorial males' reproductive success depends upon how effectively they balance competing demands to enhance fitness by choosing when to activate specific response topographies in one particular context and inhibit these same responses under different contexts. As such, inhibitory control over responding is a necessary feature of survival and fitness in *Betta splendens*.

More recently, Wooster et al. [25] proposed the *Predatory Intelligence Hypothesis*, which postulates that predator-prey interactions produce a co-evolutionary "arms race" that selects for enhanced cognitive traits such as behavioral flexibility, larger spatial/temporal memory capacity, and inhibitory control. It is this final prediction that is of primary interest for the present study. Enhanced inhibitory control offers potential survival advantages, enabling animals to assess risk more effectively, regulate territorial aggression, and optimize energy expenditure/caloric intake during foraging. During active foraging bouts, male *Betta splendens* demonstrate a well-defined predation sequence [26] once potential prey are detected [28]. Initial responses typically include slow movements and coasting toward the potential prey while the predator fish remains undetected [26]. Once potential prey are identified and localized, the predator fish waits until the closing distance to the prey is small enough that predatory attack in the form of a suction movement results in prey capture [29–32]. To successfully execute this series of responses, the fish must inhibit its suction feeding response until the moment to perform the predatory attack is optimal. There is a notable sex difference in this response; in male *Betta splendens*, the gap is 1 gape-length, whereas the gap for female *Betta splendens* is 1.5 gape-lengths [33] Therefore, foraging *Betta splendens* are capable of delaying action before acquiring prey, and the capacity for sustaining the duration of this delayed action may be stronger in males than females. While wild *Betta splendens* function as predators on a variety of small aquatic prey [34,35], they are also subject to predation pressures as prey for avian predators, such as egrets and kingfishers [36]. As a result, *Betta splendens* are subjected to bi-directional selection pressures via predator-prey interactions, which could further drive selection for enhanced cognitive capabilities, perhaps including the capacity for behavioral self-control.

Given the existing evidence across diverse taxa as well as several interrelated theoretical and empirical foundations, even domesticated *Betta splendens* may have the capacity for behavioral self-control. First, research has shown that the ability to delay gratification is not limited to mammals but

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extends to ecologically diverse non-mammalian species, including birds, cephalopods, and teleost fish [5,13,16,18] and even other invertebrates [11–13]. Second, both the *Life History Hypothesis* and the *Predatory Intelligence Hypothesis* suggest that species under complex ecological and social selection pressures, such as territorial defense, courtship, foraging, and predator avoidance, are more likely to evolve cognitive traits that could include inhibitory and behavioral self-control [21,24,25]. In the wild, *Betta splendens* males are frequently required to suppress one behavior (e.g., aggression) in favor of another (e.g., courtship) depending on the social context, indicating a capacity for context-dependent behavioral regulation [21,24]. Additionally, their foraging strategies involve precise motor inhibition during predatory strikes, further supporting the presence of temporally extended self-control processes [29–31,33]. Taken together, these patterns support the conjecture that male *Betta splendens* possess the neurobehavioral substrates necessary for behavioral self-control. Therefore, if such cognitive regulation is evident during ecologically relevant tasks, it follows that domesticated *Betta splendens* may also display this ability in a controlled experimental context involving delayed gratification.

Experiment I for the present study tests the hypothesis that domesticated male *Betta splendens* are capable of self-control by assessing whether they will opt for a larger, delayed food reward over a smaller, immediate one in a binary choice task, thereby providing critical insight into the evolutionary underpinnings of inhibitory control in a solitary teleost fish species. Subjects in Experiment I were tested in a discrete-choice instrumental response task similar to Craft et al. [37], to determine if domesticated male *Betta splendens* will demonstrate stable choice distributions for a larger-later food reward option over a smaller-sooner option; furthermore, domesticated female *Betta splendens* were also tested to determine if any sex differences exist in such choice distributions.

2. Experiment I: Materials and Method

2.1. Animals and Housing

The experimental subjects (N = 95, 52 males and 43 females) were adult, domesticated *Betta splendens* (> 6 months of age, approximately 6 cm long) obtained from a local retail supplier. Upon arrival at the facility, animals were dip-transferred from their transport cups into the experimental apparatus tank (see following section). Each tank was filled with dechlorinated tap water with water temperatures maintained at 25°C (75.2 °F) ± 1°C. All fish were kept under a 12L:12D photoperiod and fed daily with nine food pellets ("Betta Bio-Gold Baby Pellets", Hikari, Himeju, Japan). All housing, caretaking, and other procedures involving the animals were conducted in accordance with the National Research Council's [38] guidelines for the care and use of animals.

2.2. Materials and Apparatus

Fish were housed in a custom-built acrylic T-mazes based upon modifications to the designs used by Craft et al. [37] and Bols and Hogan [39]. Unlike the double-ended T-mazes used by these previous researchers with a separate start box, runway, and goal box, the individual T-mazes for Experiment I consisted of a single goal box (20.3 x 7.6 x 10.8 cm) and a combined start box/runway (20.3 x 10.2 x 10.8 cm). Each subject was housed in one end of the T-maze with a fixed opaque barrier separating T-mazes such that subjects could not see each other. Fourteen T-mazes (two per tank) were used with a subject housed separately in each T-maze, allowing for subjects to be run in squads of 14 subjects at a time. T-mazes were partially submerged to a depth of 10 cm (approximately 29 liters) within a larger polycarbonate tank (65 x 45 x 15 cm). In addition to the two T-mazes, each tank was equipped with a gravel floor, a temperature gauge, a submersible heater, and a small air stone connected to a compressed filtered air supply. During trials, a removable black T-maze divider and a choice door featuring a circular opening for each side of the divider (diameter = 2.54 cm) were used (see Figure 1). One half of both the choice door and the T-maze divider was covered with white and blue checkered-pattern contact paper, while the other side of the choice door and the T-maze divider was solid black. The checkered pattern choice door was associated with the delivery of larger-later

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food reinforcement, while the solid black choice door was associated with the smaller-sooner delivery of food reinforcement.

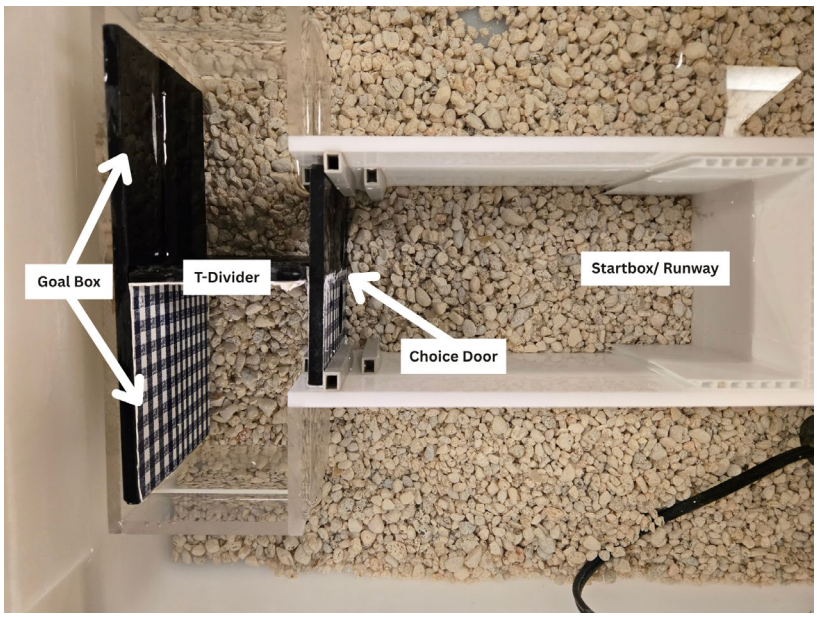

Figure 1. Overhead image of T-maze apparatus as setup for a trial. Between trials, each subject was housed within its respective T-maze without the T-divider, choice door, or start door (not pictured). At the beginning of each trial, the experimenter waited until the subject was located in the startbox/runway and placed the start door in front of the location for the choice door, followed by the choice door and T-divider.

2.3. Procedure

Prior to the start of experimental trials, fish were acclimated within the T-maze apparatus for 2 days. Trials were performed daily at 9 am, 12 pm, and 3 pm, including weekends. During each trial, subjects swam into the start box/runway and were separated from the goal box by lowering a guillotine door. During this time, the choice door and T-maze divider were inserted into the goal box behind the guillotine door. The left-right orientation of the T-maze divider was randomly alternated across trials, ensuring that the checkered pattern appeared on various sides to control for side bias. Once the T-maze divider and choice door were placed in the tank, the guillotine door was raised, and the subject was allowed to choose between the solid black or blue checkered side by swimming through the corresponding choice door opening. The amount of time the subject spent in the runway after the guillotine door was lifted was measured. Once the subject swam through a choice door, the guillotine door was closed against the choice door so that the subject could not reenter the runway during the trial or enter the other side of the T-maze divider. Once in the goal box, the subject received a manually delivered reward based on the side selected, either one pellet immediately (solid black) or three pellets after a 15-second delay (blue checkered). Subjects remained in the choice box until all pellets of food were consumed. Subjects continued to complete trials every day until stability was reached (8 out of the last 10 trials resulted in the same selection of a particular reward condition), and subjects could not demonstrate any side bias and satisfy the stability criterion. Subjects were given a maximum of 45 trials (15 days) to reach stability The 5-minute mark indicated that a subject made no choice, at which time the trial was ended and the T-maze divider and choice door were removed. During the first 15 trials of acquisition, forced-choice trials were implemented when necessary to ensure subjects experienced both reward conditions of the experiment. If the subject selected the same reward option throughout five consecutive trials, the opening of the choice door for that option was blocked, forcing the subject to choose the alternative reward condition during the forced-choice trial. Forced-choice trials were implemented to ensure all subjects were exposed to both the smaller-sooner and larger-later reward conditions, reducing the potential risk of early choice biases that could affect

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performance [40]. Prior research has demonstrated that *Betta splendens* are sensitive to trial structure, and forced-choice trials reduce potential confounds associated with habitual or consummatory-primed responses [41]. After the first 15 trials, no further forced-choice trials were conducted to allow subjects to demonstrate stable choices. Based upon the daily choice selections of each subject (1 or 3 pellets per trial, maximum of 9 pellets per day), subjects were provided 0 to 6 supplemental pellets in the afternoon to bring their total intake to 9 pellets each day.

A total of 24 subjects, 12 males (23%) and 12 females (27%), $z = 0.4493$, $p = 0.65$, either failed to reach stability or experienced health issues, and subsequently were removed from Exp. I. Data from the remaining 71 subjects were analyzed using SPSS 28.0 for Windows.

The protocols for this research were approved by the Christopher Newport University Institutional Animal Care & Use Committee (#2017-6, #2020-6, #2023-8).

3. Experiment I: Results

A total of 40 male subjects reached stabilization criteria, with 28 demonstrating a stable choice for the larger-later reward and 12 demonstrating a stable choice for the smaller-sooner reward option. Male subjects made significantly more larger-later choices than smaller-sooner choices, χ^2 (1, $n = 40$) = 6.4, $p = 0.011$. A total of 31 female subjects reached stabilization criteria, with 16 female subjects stabilized on the larger-later reward option while 15 female subjects stabilized on the smaller-sooner reward option; females had no significant stable choice distributions for larger-later choices over smaller-sooner choices, χ^2 (1, $n = 31$) = 0.032, $p = 0.858$ (see Figure 2).

Figure 2. Stable choice distributions for larger-later versus smaller-sooner reward options among male and female subjects that reached stabilization criteria. Male subjects showed a stable choice for the larger-delayed reward option, whereas female subjects showed nearly equal stable choice for either of the reward options.

Trials-to-Criterion were entered into a 2 (Sex: Male or Female) x 2 (Choice Stability: Impulsive or Self-Control) factorial ANOVA. There were no main or interaction effects of Sex or Stability, all *F*s (1,67) ≤ 2.17, *p*s ≥ 0.146. The mean number of Trials-to-Criterion across all subjects was $M = 37.5$ trials, $SEM = 1.63$ trials. At three trials per day, it typically took subjects 13-14 days to demonstrate stable choice distributions.

Response latencies across all Trials were blocked and averaged to form ten equal deciles. An Exploratory 2 (Sex) X 2 (Stability Choice: Impulsive or Self-Control) X 10 (Decile) mixed-factorial ANOVA did not reveal any main or interaction effects involving Stability Choice on response latencies, all *F*s < 1.0. Data were collapsed across Stability Choice and response latencies were

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analyzed in a 2 (Sex) x 10 (Decile) mixed-factorial ANOVA. Analysis of choice response times revealed a significant mixed-factor interaction of Decile x Sex on response latencies, $F(9, 621) = 3.73$, $p = 0.015$, $\eta_p^2 = 0.051$. Furthermore, main effects were found for both Sex, $F(1, 69) = 7.78$, $p < 0.007$, $\eta_p^2 = 0.10$, and Decile, $F(9, 621) = 13.11$, $p \leq 0.001$, $\eta_p^2 = 0.16$ (see Figure 3). Across deciles, male subjects had a longer mean response latency ($M = 31.4$ s, $SEM = 4.08$ s) than female subjects ($M = 14.2$ s, $SEM = 4.6$ s). Furthermore, subjects had significantly slower mean response latencies during the first three deciles of acquisition ($M = 41.3$ s, $SEM = 7.7$ s) than during the last three deciles of choice stability ($M = 12.1$ s, $SEM = 1.3$ s). The Decile x Sex interaction revealed significantly larger response latencies for male subjects compared to female subjects during acquisition deciles 1-2, while there was no significant difference between the response latencies of male and female subjects during the final deciles 8-10 (See Supplement 3 for a table of pairwise comparisons).

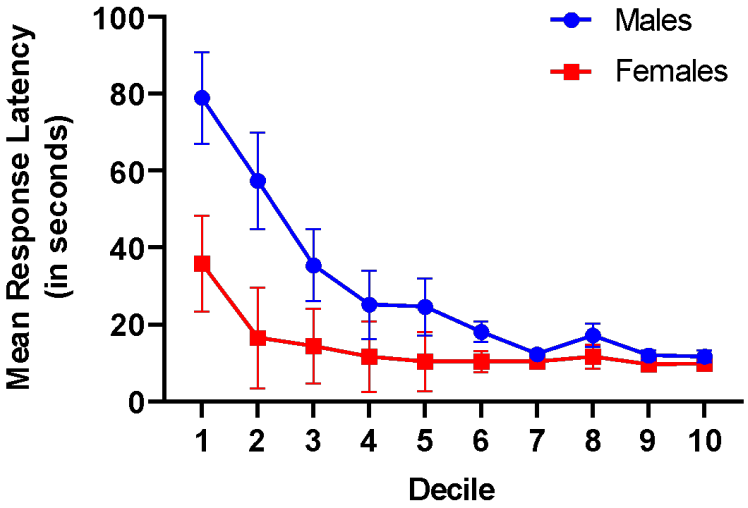

Figure 3. Mean response latencies (in seconds) across trial deciles for male and female subjects demonstrating the interaction of subject sex and deciles. While male subjects had longer response latencies during acquisition, there were very little differences between male and female subjects' response times at stable performance. Error bars represent ± 1 SEM.

4. Experiment I: Discussion

The findings of Experiment I indicate that domesticated male *Betta splendens* possess the capacity for behavioral self-control. A majority of males (~70%) demonstrated a stable choice for the larger, delayed food reward over the smaller, immediate one, indicating a group-level bias toward delayed gratification. While a subset of male subjects (~30%) displayed impulsive choice for the smaller, immediate food reward over the larger, delayed one, the dominant pattern of behavior reflected the males' ability to suppress short-term impulses for long-term benefits. These findings support theoretical predictions from the *Life History Hypothesis*, which posits that ecologically grounded trade-offs (e.g., between aggression and courtship) require context-dependent behavioral regulation [21,24]. This is further supported by the *Predatory Intelligence Hypothesis* [25], which suggests that precise predatory strike timing requires motor inhibition and decision latency, both of which are core components of behavioral self-control. In contrast, female subjects showed a near-equal split among choice for delayed versus immediate rewards, with no statistically significant group-level bias towards one option over the other. This indifference at the group level may reflect underlying ecological distinctions between sexes in natural contexts. Unlike males, female *Betta splendens* are non-territorial and tend to forage opportunistically, moving between male territories rather than defending fixed resources [22,23]. Consequently, the selective pressure on inhibitory control may be

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weaker in females. These sex-specific behavioral tendencies mirror those reported in other taxa, such as cleanerfish and parrots, where ecological roles shape the development of behavioral capacities [18,42,43].

5. Experiment II: Introduction

Given the observed behavioral self-control in male, but not female, domesticated *Betta splendens*, the second experiment was designed to study a potential neurochemical mechanism underlying the proximate basis for self-control as it pertains to reward valuation and motivated responding. In mammals, the mesolimbic dopaminergic pathway originates in the ventral tegmental area (VTA) and projects to the nucleus accumbens (NAcc), amygdala, and hippocampus. This pathway plays a central role in reinforcement learning, reward valuation, and inhibitory control [44]. While there are substantial differences between mammals and the teleost fishes regarding brain structure and organization (for a review, see [45]), comparative investigations have identified putative homologs of mammalian mesolimbic structures, primarily within the teleost telencephalon (see Table 1). Recently, Dupeyron and Wallace [46] conducted social exposure experiments with domesticated male *Betta splendens* to combine behavioral assessments with neuroanatomical study to identify and confirm various telencephalic regions in the fish brain implicated in opponent recognition. While Dupeyron and Wallace used a social behavioral assay, their findings confirmed several neuroanatomical and functional homologies in the brain of domesticated *Betta splendens*. Mammalian components of the dopaminergic mesolimbic pathway include the dorsolateral telencephalon (Dl), the dorsomedial telencephalon (Dm), and the ventral portion of the ventral telencephalon (Vv). While several neurotransmitters play a role in the activity of the mesolimbic pathway, dopamine is the primary neurotransmitter and is found to be highly conserved across vertebrate species [47,48] (for a review, see [49]). Furthermore, DOPA decarboxylase, responsible for catalyzing L-Dopa into dopamine, is also highly conserved across vertebrate species [47,50]. Relevant to the current study, the role of dopamine regarding reward valuation in mammals and birds is well established [51–54]. While there is less literature regarding the role of dopamine in reward valuation specifically in teleost species, let alone in *Betta splendens*, dopamine appears to play a role in reward-mediated learning in cleaner wrasse, *Labroides dimidiatus* [55], conditioned place-preference in zebrafish, *Danio rerio* [56], Pavlovian conditioning of unconditional social reward in zebrafish, *Danio rerio* [57], reversal learning in rainbow trout, *Oncorhyncus mykkiss* [58] and aggression induced by omission of expected reward in Atlantic salmon, *Salmo salar L.* [59]. Finally, Collins and Frank [60] suggest that dopaminergic responses to reward can be attenuated by either delay or infrequency, and enhanced dopaminergic activation occurs more strongly with immediate or more frequent rewards. This hypothesized effect can be studied, in part, by administering either a dopamine precursor (e.g., L-Dopa) or a dopamine agonist (e.g., apomorphine).

Table 1. Comparative table of mesolimbic structures in mammals to homologs in fish.

Mammalian Brain Region	Function	Fish Homolog	Evidence
Ventral Tegmental Area (VTA)	Source of dopaminergic projections to forebrain (reward, motivation)	Posterior tuberculum (TPp)	Dopaminergic neurons in TPp project to telencephalic targets, functionally similar to VTA [61]
Nucleus Accumbens (NAcc)	Integrates dopaminergic signals (reward processing)	Ventral part of the ventral telencephalon (Vv/Vd)	Gene expression (e.g., dopamine receptors, neuropeptides), connectivity, behavioral roles [62]

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Amygdala	Emotion, social behavior, fear processing	Medial and dorsal parts of the ventral telencephalon (Dm)	Dm is involved in fear, aggression, and social learning in fish [63]
Hippocampus	Learning and memory	Dorsolateral telencephalon (Dl)	Homologous by gene expression (e.g., *zic1*, *emx*), lesion studies, and spatial tasks [64]

Rutledge et al. [65] and Pine et al. [66] both investigated the effects of L-Dopa on choice responding in humans, finding that increased dopamine influences risk sensitivity and impulsive responding. Rutledge et al. [65] administered L-Dopa or a placebo to healthy young adult humans and found that participants made riskier economic choices and favored short-term rewards after receiving L-Dopa. Similarly, Pine et al. [66] employed a within-subject design, in which healthy adult humans received L-Dopa, haloperidol, or placebo across sessions while completing an adjusting-delay task, in which they chose between smaller-sooner and larger-later rewards. Pine et al. [66] found that L-Dopa led to a greater stable choice for immediate rewards, indicating increased impulsivity, while haloperidol had no significant effect. Together, these studies suggest that L-Dopa enhances dopaminergic activity and shifts responding toward riskier and more impulsive choices in humans. Interestingly, patients with Parkinson's disease and other conditions treated with L-Dopa (i.e., generic Levodopa) or dopamine agonists (e.g., generic Apomorphine HCL) often display gambling addiction, impulsiveness, and increased risk seeking [67]. In their review, Santanegelo et al. [67] suggest that the delivery of dopamine precursors/agonists in humans reduces the output strength of frontostriatal connections (associated with impulse control in the frontal cortex) and increases the output strength of striatal connections (associated with impulsive drive and a consistent choice for immediate rewards). In addition to tremors activated by the nigrostriatal motor pathway due to the loss of dopaminergic neurons in the substantia nigra, patients with Parkinson's disease often present with diminished executive control and reduced capacity for self-monitoring. The prevalence of pathological gambling and other impulse-control disorders is notably higher in patients with Parkinson's disease than in the general population [67]. Multiple studies indicate a strong association between dopamine therapies, including pharmacological Levodopa, and pathological gambling [68–70]. However, it is important to note that indirect dopamine agonists such as methylphenidate are well-established pharmacotherapies used in the reduction of impulsiveness in ADHD and other similar disorders, e.g., [71] (for reviews, see [72,73]. These findings collectively underscore the central role of endogenous dopamine in modulating impulsive response and highlight the potential for dopamine-enhancing agents, such as exogenous L-Dopa, to affect behavioral self-control in humans and possibly in other animals. As such, the development of an animal model of dopamine-induced impulsiveness could be helpful for biobehavioral researchers.

Given the demonstrated capacity for behavioral self-control by the male Betta splendens in Experiment I and Dupeyron and Wallace's [46] recent characterization of the relevant regions in *Betta splendens*, which are likely homologs to the dopaminergic mesolimbic pathway in mammals, this dopaminergic signaling likely plays an essential role in reward-based choice behavior in *Betta splendens*. The behavioral effects of L-Dopa in human participants, especially increased impulsivity, choice for immediate rewards, and diminished self-control, suggest that artificially increased dopamine levels create a bias towards stable choices of short-term rewards. If these effects are conserved across vertebrate taxa, then male *Betta splendens* receiving oral L-Dopa should exhibit a behavioral shift towards stable choice for smaller, immediate reward in the discrete-choice instrumental choice task. Specifically, L-Dopa administration is expected to reduce choice latency, especially during the acquisition phase, and increase impulsive choice. Experimental confirmation of this hypothesis would provide compelling evidence for the conservation of the dopaminergic mechanisms underlying impulsive choice and establish *Betta splendens* as a potential model organism for investigating the neural bases of reward valuation, choice, and impulsiveness/self-control.

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6. Experiment II: Materials and Method

6.1. Animals and Housing

The subjects (N = 82) were healthy male adult Siamese Fighting Fish (domesticated *Betta splendens*) obtained from the same local supplier. Housing and husbandry were the same as Experiment 1.

6.2. Procedure

Upon arrival at the facility, each subject was weighed (M = 1.12 g, SEM = 0.03 g), and subjects were subsequently matched in pairs ($Npairs$ = 33) based upon weight (weights were used for subsequent dosage calculations). Following the matching procedure, one subject was randomly assigned to the L-Dopa treatment condition while the corresponding member of the pair was assigned to the vehicle-only control condition. An additional 16 subjects were run in the L-Dopa condition (N = 49). For both vehicle and vehicle + L-Dopa delivery, custom food-based pellets were made using ground fish feed (Cichlid Gold Floating Type Mini Type, Hikari, Japan) mixed in a slurry of either RO water or RO water plus L-Dopa (CAS# 53587-29-4, Sigma Aldrich, Inc., St. Louis, MO, USA). The concentration of the L-Dopa was calculated to yield a 60 mg/kg dose of L-Dopa in these small pellets (M = 0.95 mg, SEM = 0.12 mg). Following preparation, pellets were dessicated overnight and weighed (M = 0.95 mg, SEM = 0.12 mg) to ensure uniformity. The 60 mg/kg dosage was selected based upon pilot trials with male *Betta splendens testing* 40, 60, and 80 mg/kg doses in which 80mg/kg, but not 60 mg/kg, induced erratic swimming and hypermotility, likely indicative of dyskinesia and consistent with the finding that 80 mg/kg induced dyskinesia in primates when given orally [74]. Furthemore, we did not include a peripheral decarboxylase inhibitor such as carbidopa in our L-Dopa pellets. As a result, the exogenous L-Dopa was likely metabolized at a higher rate [75], especially in the periphery. This necessitated the use of the maximum possible dose that would not induce dyskinesia. Thirty minutes prior to the start of each trial, subjects were given either a ~1 mg vehicle pellet or an ~1 mg pellet with L-Dopa, and subjects were given 10 minutes to consume the pellet. If the subject failed to consume the pellet during the acquisition phase of Experiment II, the trial continued regardless. However, subjects were required to fully consume every pre-trial pellet during the performance phase of Experiment II to demonstrate stable choice; the stability criterion stipulated that subjects consume every pre-trial pellet for the final 10 trials of the experiment. Animals that failed to consume pre-trial pellets on more than 5 consecutive or non-consecutive occasions were also excluded from Experiment II. While the pre-trial pellet was necessary for oral administration of L-Dopa + vehicle or vehicle alone, it also served to slightly reduce variability in hunger and reward motivation between subjects in Experiment II. All remaining procedural aspects of Experiment I were used identically in Experiment II.

A total of 26 subjects, 10 subjects in the vehicle-only group (30.3%) and 16 subjects in the L-Dopa group (32.7%), z = 0.229, p = 0.8181, either failed to reach stability or experienced health issues that resulted in their removal from the study. Data from the remaining 56 subjects were analyzed using SPSS 28.0 for Windows.

7. Experiment II: Results

A total of 23 subjects in the vehicle-only control condition reached stabilization criteria, with 12 control subjects stabilized on the larger-later reward option while 11 control subjects stabilized on the smaller-sooner reward option; control subjects had no significant stable choice between larger-later rewards and smaller-sooner rewards, χ^2 (1, n = 23) = 0.043, p = 0.835. Significantly more males in Experiment 1 (n = 28/40) demonstrated behavioral self-control than males in the vehicle-only group (n = 12/23) in Experiment 2, χ^2 (1, N = 75) = 8.19, p = 0.004 (Yate's correction). A total of 33 subjects in the L-Dopa condition reached stabilization criteria, with only 10 L-Dopa subjects demonstrating a stable choice for the larger-later reward, while 23 L-Dopa subjects stabilized on the smaller-sooner

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reward option. Subjects in the L-Dopa condition had significantly fewer larger-later choices than smaller-sooner choices, χ^2 (1, n = 33) = 5.12, p = 0.024 (see Figure 4).

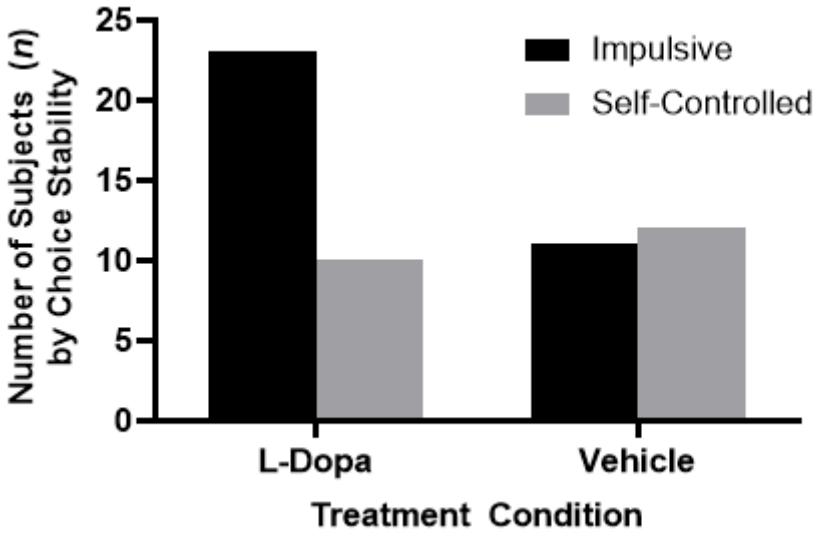

Figure 4. Stable choice distributions for larger-later versus smaller-sooner reward options among L-Dopa-treated and vehicle-only subjects that reached stabilization criteria. Significantly more L-Dopa subjects chose smaller immediate reward, while vehicle-only subjects showed nearly equal stable choice for either reward option.

Trials-to-Criterion were entered into a 2 (Treatment: Vehicle or L-Dopa) x 2 (Choice Stability: Impulsive or Self-Control) factorial ANOVA. There were no main or interaction effects of Sex or Stability, all Fs (1,67) ≤ 2.17, ps ≥ 0.146. The mean number of Trials-to-Criterion across all subjects was M = 24.9 trials, SEM = 1.11 trials. At three trials per day, it typically took subjects 8-9 days to demonstrate stable choice distributions. Subjects in Experiment II reached stability in significantly fewer trials than subjects in Experiment I, t(125) = 6.04 , p ≤ 0.0001.

Response latency across all Trials were blocked and averaged to form ten equal deciles. An exploratory 2 (Sex) X 2 (Stability Choice: Impulsive or Self-Control) X 10 (Decile) mixed-factorial ANOVA did not reveal any main effect, F(1,50) = 1.30, p = 0.259, or interactions involving Stability Choice, all Fs (9,450) ≤ 1.26, ps ≥ 0.259, on response latencies. Data were subsequently collapsed across Stability Choice and response latencies were analyzed in a 2 (Treatment Condition) x 10 (Decile) mixed-factorial ANOVA. There was a significant mixed-factor interaction of Deciles x Treatment Group, F(9,468) = 2.441, p = 0.010, η_p^2 = 0.045 (see Figure 5 and Supplement 3 for a table of pairwise comparisons) as well as a main effect of deciles on response latencies with significantly faster response times in later deciles, F(9, 468) = 18.35, p < 0.001, η_p^2 = 0.261 (see Figure 4). There was no significant main effect of treatment condition on response latencies, F(1, 52) = 1.093, p = 0.301, η_p^2 = 0.021

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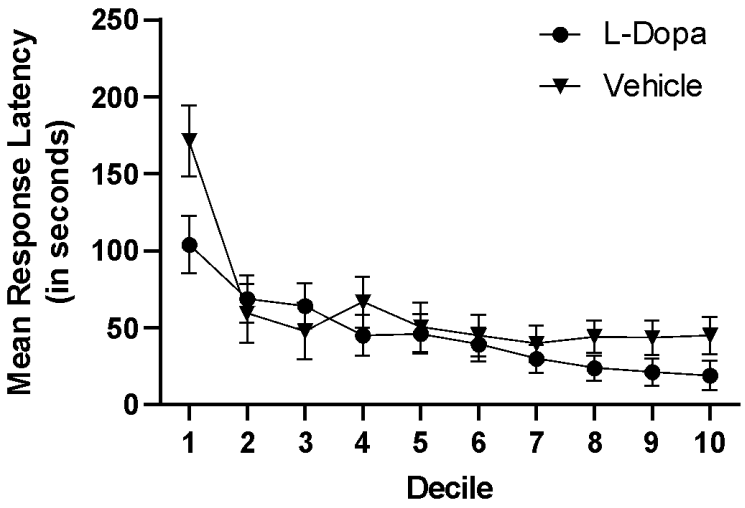

Figure 5. Mean response latencies (in seconds) across trial deciles for L-Dopa-treated and vehicle-only subjects. L-Dopa-treated subjects had shorter response latencies during the initial decile of acquisition, but very little difference with Vehicle-only subjects during the remainder of acquisition and performance. Error bars represent ± 1 SEM.

8. Experiment II: Discussion

The results of Experiment II support the hypothesis that increased dopaminergic activity disrupts behavioral self-control in male *Betta splendens*, as subjects administered oral L-Dopa had a stable choice for the smaller-sooner reward, consistent with impulsive responding [65,66]. However, males in the vehicle-only group did not demonstrate a significant stable choice for the larger-later reward, unlike the substantial majority of male subjects in Experiment I. Rather, the males in the vehicle-only group displayed a choice distribution similar to the female subjects in Experiment I, that demonstrated no group-level stable choice bias. This particular finding suggests that administering a small, consumable, and unearned reward before each trial may alter baseline reward choice behavior in the discrete-trial instrumental choice task. Furthermore, the similarity between the vehicle-only male subjects in Experiment II and the female subjects in Experiment I may indicate either a contextual shift in motivational state or a reduction in the ecological relevance of the reward contingencies under a slightly modified procedure. Notably, the L-Dopa subjects' stable choice for immediate reward was significantly greater than the indifference demonstrated by the vehicle-only group, indicating that the dopaminergic manipulation produced the shift to impulsive choice in the experimental group. These findings are further supported by the Decile by Treatment Group interaction in response latencies, where L-Dopa-treated subjects exhibited faster response latencies at the beginning of the acquisition phase and again during the performance phase, a pattern consistent with reduced response processing and increased impulsive responding [51,60]. Taken together, these findings indicate that dopamine plays a central and evolutionarily conserved role in modulating behavioral self-control in *Betta splendens*.

9. General Discussion

Across Experiments I and II, the current study demonstrates that domesticated male *Betta splendens* exhibit a stable and observable capacity for behavioral self-control in the discrete-choice instrumental response task. This capacity is disrupted by the administration of oral L-Dopa. In Experiment I, males demonstrated a substantial stable choice for the larger-later reward option over the smaller-soon alternative; 70% of males stabilized on the delayed-reward option. This behavioral capacity is further demonstrated by the significantly longer response latencies among male subjects

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during the early acquisition phase of the experiment, which provides a pattern of responding consistent with behavioral self-control [2,3,6]. In contrast, female subjects in Experiment I did not demonstrate any group-level stable choice for either reward option, and their response latencies were shorter and more stable across deciles, suggesting less engagement of response inhibition during experimental trials. These sex differences are consistent with the *Life History Hypothesis* [19] and ecological observations that male *Betta splendens*, as territorial and selective foragers, are under stronger selection pressures that favor behavioral inhibition [21,22]. In the wild, male *Betta splendens* must frequently suppress aggression to engage in courtship with receptive females or to surface-feed and tend fertilized eggs in their bubble nest. Additionally, males must delay predatory strikes for optimal timing during prey acquisition and regulate energy expenditure during courtship, foraging, and defense; collectively, these response patterns involve behavioral self-control [25,29,33].

In Experiment II, administration of oral L-Dopa to the experimental group produced a marked shift towards impulsive choice. While the vehicle-only group demonstrated group-level indifference in stable choice with a nearly equal distribution between smaller-sooner and larger-later options, similar to the female subjects in Experiment I, the L-Dopa group showed a significant stable choice for the smaller-sooner reward, consistent with increased impulsivity. Notably, this shift in choice was accompanied by a significant interaction between decile and treatment, where subjects in the L-Dopa condition exhibited shorter response latencies during both the early acquisition and later performance phases of the experiment, consistent with increased impulsive action [51,60]. These findings are consistent with the results of human studies demonstrating that exogenous L-Dopa increases risky choice and diminishes tolerance for reward delays [65,66] as well as with clinical research indicating that dopamine-enhancing treatments such as Levodopa and dopamine agonists are associated with increased risks for impulse-control disorders and gambling addiction in patients with Parkinson's disease [67–70]. The results from Experiment II extend these findings to a non-mammalian vertebrate, suggesting that dopaminergic signaling modulates behavioral self-control in an evolutionarily conserved manner. It is worth noting that some dopamine agonists, such as those used to treat Attention Deficit Hyperactivity Disorder (ADHD), are successful in decreasing self control issues [71]. However, medications like methylphenidate that are used to treat ADHD act primarily as agonists at the D1 and D2 receptors in [73]. Further research is needed using D1 and D2 specific agonists and antagonists to determine the exact mechanism through which levodopa is able to inhibit self-control in male *Betta splendens.*

The results of the present study provide empirical support for the theoretical and ecological frameworks reviewed in the Introduction. Specifically, the *Predatory Intelligence Hypothesis* [25] posits that predator-prey interactions select for enhanced cognitive capacities, and our findings align with this framework. Male *Betta splendens* not only demonstrated behavioral self-control in the foraging context of the discrete-trial instrumental choice task, but their performance was modulated by manipulation of the dopaminergic system. These results add to the growing body of literature suggesting that self-control and delay of gratification are not uniquely human or even mammalian traits, but are distributed across several taxa as driven by ecological demands [8,13,16,18]. Furthermore, the functional dopaminergic homologies between fish telencephalic regions and mammalian mesolimbic structures provide a neurofunctional basis for the observed parallels in these behaviors across taxa [47,62,64]. Within this framework, *Betta splendens* can serve as a viable comparative model for further study on the neural substrates of reward valuation and behavioral regulation.

Nonetheless, the current study has several limitations that should be noted here. First, we acknowledge the potential confound introduced by the assignment of the checkerboard pattern to one reward condition and the black pattern to the other reward condition. However, other researchers [76,77] have also used a checkerboard pattern similar to the one of the current study as a discriminative stimulus during instrumental response tasks with *Betta splendens* and did counterbalance the assignment of the discriminative stimuli with their specific reward conditions. These previous studies did not detect counterbalancing effects or interactions involving the

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checkerboard pattern. Given the consistency of this evidence and the ethical consideration to avoid unnecessary increases in the number of animals used in research [78], we chose not to counterbalance. Secondly, while the results support the conclusion that endogenous L-Dopa increases impulsivity by increasing dopamine levels in the aforementioned pathway, the present study does not include a dose-response curve or multiple pharmacological manipulations (e.g., direct dopamine agonism or antagonism) to more fully characterize the extent to which dopamine plays a role in reward valuation and behavioral self-control in *Betta splendens*. It is also important to note that daily oral administration of L-Dopa in the present study occurred with a 3-hour interval from the morning to the mid-day trial and again from the mid-day to the afternoon trial, so a small carryover effect may have occurred throughout each experimental day. As L-Dopa has a short half-life of approximately 50 minutes in humans [75], the effective clearing would be approximately 12.4x (down to ~4.9 mg/kg) between the daily trials. Furthermore, L-Dopa is the precursor for not only CNS dopamine, but for other catecholamines in both the CNS and the periphery. Of particular note is the likelihood that the L-Dopa intervention in Experiment II also increased peripheral norepinephrine as norepinephrine plays an important role in stress-mediated responding in fish [79]. As such, the potential elevation of peripheral norepinephrine in the experimental subjects of Experiment II could have resulted in a stress-mediated reduction of inhibition which could, in turn, increase impulsivity. Additionally, the procedural differences between the two experiments, particularly the administration of a small, unearned food pellet before each trial in Experiment II, may have altered motivational drive or reward salience in the vehicle-only group, thereby reducing comparability across the two experiments. Finally, only male subjects were used in Experiment II, as they demonstrated behavioral self-control in Experiment I. Future work should explore the extent to which female *Betta splendens* exhibit similar dopaminergic modulation when tested under similar pharmacological conditions.

In addition to addressing the previously-mentioned limitations, future research can expand upon the current findings. For example, follow-up studies could explore a fuller range of pharmacological manipulations across dose ranges, dopamine antagonists, or selective D1v/D2v receptor agents to better characterize the receptor-specific aspects of dopaminergic regulation of behavioral self-control. The use of D1v/D2v receptor agents as well as specific noradrenergic agents could also aid in disentangling the potential that levodopa is also increasing noradrenergic activity that is relevant to the observed behavior. In addition, activity in telencephalic regions homologous to the mammalian mesolimbic pathway could be assessed with molecular techniques, e.g., immediate early gene expression, following demonstrated stable choice in order to provide more direct evidence of neural pathway involvement. To address the lack of a dose-response curve in the present study, future experiments could examine the effects of several doses of L-Dopa on both response topography during acquisition and performance as well as choice distributions between smaller-sooner and larger-later rewards. Such research should include the combination of carbidopa with L-Dopa to inhibit the action of decarboxylase to reduce the enzymatic conversion of L-Dopa to other catecholamines in the periphery and increase the availability of L-Dopa for CNS effects. Future researchers could also study wild-type *Betta splendens* or other teleost species from various ecological niches to determine how environmental and selection pressures shape response traits such as behavioral self-control. Furthermore, while the current study demonstrates that male *Betta splendens* demonstrate behavioral self-control that is disrupted by L-Dopa, the females in Experiment I did not demonstrate reliable choice distributions in favor of either reward condition, which raises questions regarding the extent to which dopamine plays a similar modulatory role in reward valuation by females. As such it would be very interesting to study the effects of dopamine agonists or antagonists on female *Betta splendens* to explore whether the apparent indifference in reward valuation is due to baseline neurochemical differences, reduced dopaminergic sensitivity, or alternative motivational frameworks shaped by the females' non-territorial ecological roles. For instance, females could likely exhibit increased stability in SS choice under L-Dopa, due to their opportunistic nature relying on convenience of resources. This hypothesis could be tested using the same methods from Experiment II, creating a direct comparison between male and female *Betta splendens'* choice behavior under

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dopaminergic manipulations. Finally, other behavioral approaches such as effort-based choice responding, probabilistic reward tasks, or response inhibition, (e.g., the five-choice serial reaction time task [80] combined with various bioassays would provide broader understanding of how dopamine and other catecholamine systems influence aspects of reward-mediated responding in teleost species [61]. Collectively, these future directions could establish domesticated *Betta splendens* as a useful model for studying the evolution and neurobiology of behavioral self-control across vertebrates.

10. Conclusions

The present study demonstrates that domesticated male *Betta splendens* exhibit a clear capacity for behavioral self-control, as evidenced by their stable choice for larger, delayed rewards in a discrete-choice instrumental task, and that this capacity can be disrupted by oral administration of L-Dopa. The findings provide support for the *Life History Hypothesis* and the *Predatory Intelligence Hypothesis* by showing that males, but not females, display a stable choice for delayed rewards, consistent with the ecological pressures faced by territorial males in the wild. Moreover, Experiment II revealed that enhancing dopaminergic activity via oral L-Dopa shifted male behavior toward impulsive choice, paralleling human and clinical findings linking dopamine increases to impulsivity and risk-taking. These results highlight the evolutionary conservation of dopaminergic mechanisms involved in reward valuation and inhibitory control, reinforcing the functional homologies between fish telencephalic regions and the mammalian mesolimbic pathway. While additional research is necessary to explore dose-response effects, receptor-specific mechanisms, and sex differences under pharmacological manipulation, the current findings establish a foundation for comparative studies on the neural substrates of decision-making. As such, domesticated *Betta splendens* are a promising animal model for investigating the neurobiological bases of impulsiveness and behavioral self-control.

Supplementary Materials: The following supporting information can be downloaded at the website of this paper posted on Preprints.org.

Author Contributions: Conceptualization, A.V. and K.W.; methodology, A.V.; software, N/A; validation, A.V.; formal analysis, A.V.; investigation, K.W., N.W., A.A., G.D-A., I.T., B.W. and K.K.; resources, A.V. and K.W.; data curation, A.V; writing—original draft preparation, A.V., K.W., N.W., A.A., G.D-A., I.T., and B.W.; writing—review and editing, A.V., K.W., N.W., A.A., G.D-A., I.T., B.W., and K.K.; visualization, A.V.,, K.W., and K.K.; supervision, A.V.; project administration, A.V., K.W., N.W., A.A., and G.D-A.; funding acquisition, K.W. and G.D-A. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data presented in this study are available upon request from the corresponding author.

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well as reviewing clarity and cohesion in the Introduction and Discussion sections. The authors have reviewed and edited the output and take full responsibility for the content of this publication. The graphical abstract for this manuscript was created in BioRender v 1.0 by Kinslow, K. (2025). https://BioRender.Com/npm45jc (11 September, 2025)

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