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ORIGINAL ARTICLE

The role of serotonin in modulating common waxbill behaviour

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Abstract

Serotonin or 5-hydroxytryptamine (5-HT) is a monoaminergic neurotransmitter that is known to influence behaviour in various animal species. Its actions, however, are complex and not well-understood yet. Here, we tested whether and how two 5-HT receptor agonists and a 5-HT receptor antagonist influence behaviour in common waxbills (*Estrilda astrild*), focusing on aggression, movement and feeding. We applied acute administration of either 8-OH-DPAT (a 5-HT_{1A} receptor agonist), fluoxetine (a selective serotonin reuptake inhibitor; SSRI) or WAY 100,635 (a 5-HT_{1A} receptor antagonist), and then quantified behaviour in the context of competition for food. Waxbills treated with the SSRI fluoxetine showed an overall decrease of aggressive behaviour, activity and feeding, while we found no significant effects of treatment with the other serotonergic enhancer (8-OH-DPAT) or with the antagonist WAY 100,635. Since both 8-OH-DPAT and WAY 100,635 act mainly on 5-HT_{1A} receptor pathways, while fluoxetine more generally affects 5-HT pathways, our results suggest that receptors other than 5-HT_{1A} are important for serotonergic modulation of waxbill behaviour.

Significance statement

The serotonergic system is of interest for current behavioural research due to its influence on a range of behaviours, including aggression, affiliative behaviour, feeding and locomotion in various species. There are, however, numerous discrepancies regarding the behavioural effects of serotonin across studies. We used acute pharmacological manipulations of the serotonergic system in common waxbills, using two serotonin enhancers (8-OH-DPAT and fluoxetine) and a serotonin blocker (WAY 100,635). Behavioural effects of these pharmacological manipulations on aggressiveness, movement and feeding, during tests of competition over food, indicated an anxiogenic-like effect of fluoxetine, but not of 8-OH-DPAT and WAY 100,635. This suggests a distinct role for different serotonergic pathways on waxbill behaviour.

Keywords Serotonin (5-HT) · Behavioural response · Aggression · Common waxbill (*Estrilda astrild*)

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Introduction

The behaviour of social and gregarious animals is often adapted to access and compete for resources such as food and mates within the group (Dickinson and Koenig 2018), and to establish dominance hierarchies (Drews 1993; Chase and Lindquist 2009; Paull et al. 2010; Ziomkiewicz 2016; Theodoridi et al. 2017). In many animal species, the mechanisms underlying aspects of social behaviour, including aggressive and impulsive behaviours, involve serotonergic function (e.g., Brown et al. 1979; Popova et al. 1997; Duke et al. 2013), which is a critical neural circuitry mediating context-dependent modulation of behaviour (Oliveira 2009). Serotonergic modulation can, affect multiple aspects of behaviour, including aggressive responses, mood, impulsivity, locomotor activity, affiliation and feeding, in both invertebrates and vertebrates (e.g. Evenden and Ängeby-Möller 1990; Saadoun and Cabrera 2002; Tse and Bond 2002; Ögren et al. 2008; Schweighofer et al. 2008; Oliveira 2009; Crockett et al. 2010; Mennigen et al. 2010; Kiser et al. 2012; Maximino et al. 2013; Björklund Aksoy 2017; Stettler et al. 2021), including birds (Steffens et al. 1997; Sperry et al. 2003; Dennis et al. 2008, 2013; dos Santos et al. 2015).

The role of serotonin (5-HT) in aggression and its relation to other behavioural dimensions, such as affiliation, feeding or movement, can be complex, with responses often depending on species' identity, dosages used, social status or context (Hillegaart and Hjorth 1989; Evenden and Ängeby-Möller 1990; Steffens et al. 1997; Kravitz 2000; Harrison and Markou 2001; Saadoun and Cabrera 2002; Sperry et al. 2003; Gaworecki and Klaine 2008; Mennigen et al. 2010; Barry 2013; dos Santos et al. 2015; Huntingford 2019). Key experimental evidence implicating 5-HT as mediator of aggression and other behaviours have come from studies with pharmacological manipulations, designed to selectively and/or generally facilitate or to inhibit the serotonergic pathways (Tse and Bond 2002; Sperry et al. 2003; Dennis et al. 2008; Lorenzi et al. 2009; Lillesaar 2011; Maximino et al. 2013; Björklund Aksoy 2017). For instance, enhancing serotonergic function has been found to diminish aggressiveness in mammals (Olivier et al. 1995; Adams et al. 1996, Lopez-Mendoza et al. 1998), birds (Fachinelli et al. 1996; Sperry et al. 2003), fish (Winberg et al. 2001; Clotfelter et al. 2007; Dzieweczynski et al. 2016; Stettler et al. 2021), reptiles (Deckel 1996) as well as in crustaceans (Huber et al. 1997; Kravitz 2000). Suppressing serotonergic action has revealed opposite effects, with treated individuals seemingly becoming more aggressive, in a variety of model systems that include humans (Crockett et al. 2008, 2009), rodents (Lopez-Mendoza et al. 1998; de Boer et al. 1999, 2000;), birds (i.e., Buchanan et al. 1994) and fish species (Clotfelter et al. 2007; Paula et al. 2015; Stettler et al. 2021). Unsurprisingly, some discrepancies have been found between study species, treatments, dosages used and experimental contexts, as seen in Stettler et al. (2021), for example, where the agonist 8-OH-DPAT increased aggression in a cooperatively breeding cichlid (*Neolamprologus pulcher*), and the antagonist WAY 100,635 decreased aggression.

Behaviours like foraging or locomotion can also be affected by 5-HT, for example with serotonergic function reducing feeding motivation (e.g., birds: Saadoun and Cabrera 2002; fish: Gaworecki and Klaine 2008; Mennigen et al. 2010), but here too some discrepant results have been found (Steffens et al. 1997; dos Santos et al. 2015). With serotonergic enhancers like 8-OH-DPAT (agonist) and fluoxetine (a selective serotonin reuptake inhibitor, SSRI) either increasing or decreasing locomotor behaviour, depending on the study species (e.g.: rodents: Hillegaart and Hjorth 1989; Evenden and Ängeby-Möller 1990; Harrison and Markou 2001; and fish: Kohlert et al. 2012; Barry 2013; Dzieweczynski et al. 2016).

5-HT activity is affected by a large family of receptors, with the 5-HT_{1A} and 5-HT_{1B} subtypes being particularly influential in the modulation of several behaviours, including aggressiveness (e.g., humans: Nelson and Chiavegatto 2001; rodents: Olivier et al. 1995; de Boer and Koolhaas 2005; birds: Dennis et al. 2008). The 5-HT_{1A}-like receptors are divided into two distinct groups based on their neural location: i) autoreceptors, known to suppress firing of serotonergic neurons when activated, therefore reducing 5-HT activity (Sprouse and Aghajanian 1987; Polter and Li 2010; dos Santos et al. 2015); and ii) heteroreceptors, that, when activated, execute intracellular effects (Carey et al. 2004; Polter and Li 2010). However, in avian models, information on serotonergic mechanisms underlying behavioural mediation, receptors and specific pathways is yet sparse (Buchanan et al. 1994; Sperry et al. 2003; Dennis et al. 2008, 2013).

Since there is limited information on the influence of serotonergic mediation in avian behaviour, we chose to focus on its effects in the common waxbills (*Estrilda astrild*), a highly gregarious bird found in flocks year-round, roosting, allopreening and bathing communally (Clement et al. 1993; Payne 2010). The common waxbill is, therefore, ideal to study the influence of 5-HT on behaviour, as this neurotransmitter may affect the drive to be social (Young 2013). Groups of common waxbills (hereafter, waxbills) form dominance hierarchies with mildly steep slopes, meaning that dominant individuals may sometimes be displaced by lower ranked birds, and individual differences in aggressiveness can be studied with behavioural trials of competition for food (Funghi et al. 2015, 2018; Beltrão et al. 2021a). Although there are repeatable individual differences in aggressiveness

and social dominance, male and female waxbills are on average similarly aggressive and dominant (Funghi et al. 2015, 2018; Beltrão et al. 2021a, b). In this study, we focused on 5-HT_{1A} receptors due to their widespread distribution in the brain (e.g., humans: Saulin et al. 2012; pigeon, *Columba livia*: dos Santos et al. 2015). We treated waxbills with 8-OH-DPAT (a 5-HT_{1A} receptor agonist), WAY 100,635 (a 5-HT_{1A} receptor antagonist) and fluoxetine (a SSRI that prevents 5-HT reuptake) and observed their overall locomotor activity, feeding, aggressiveness and allopreening, to investigate serotonergic effects on behaviour. Following most existing studies, usually using non-avian models, we hypothesized that the agonist 8-OH-DPAT and the SSRI fluoxetine would decrease waxbill aggressiveness and increase affiliative interactions, while the antagonist WAY 100,635 would have opposite effects. Our study is one of the few done in birds and analysing both sexes.

Material and methods

Model species

We acquired 24 adult wild-type common waxbills (12 males and 12 females), aged approximately around 3–4 years, from certified breeders in September 2019 and housed them in a room with birdcages at CIBIO (Vairão, Portugal). The birds were ringed for individual identification and housed in six cages, in mixed-sex groups of 4 birds per cage (2 males and 2 females), remaining in each designated cage until the end of experiments. These metal cages (88.5 × 30 × 40 cm) had 4 perches and a gridded front (Fig. 1). The room had natural ventilation, temperature, and light, complemented with light from full spectrum lamps on the ceiling, on a cycle adjusted to the natural photoperiod (lights on ca. 30 min before sunrise, and off ca. 30 min after dawn). The birds were provided with ad libitum food (a commercial mix of seeds for exotics birds, *Tropical Finches Prestige*, Versele-Laga, composed by panicum yellow 42%, yellow millet 28%, japanese millet 11.5%, canary seed 8,5%, red millet 5%, panicum red 4%, niger seed 1%), water in two drinkers, mixed grit with crushed oyster shells (*Grit with Coral Prestige*, Versele-Laga) on the cage floor, to provide a calcium supplement, and bathtubs were made available twice a week.

Manipulation of the 5-HT system and experimental design

Experiments took place between September and November 2019, corresponding to the non-reproductive season of waxbills in the Iberian Peninsula (Sanz-Aguilar et al. 2015; Beltrão et al. 2021c). Also, for consistency, experiments took place during the morning, between 9:30am and 12:45 pm, since birds are generally more active during the morning, and to avoid hormonal variations that occur along the day. Two hours before each behavioural test, we food deprived birds by removing all feeders from a cage. After 1h40min of food deprivation, each bird of the same cage was briefly removed to receive an injection, with treatments scheduled in a balanced manner through time (see supplementary material Table A.1). Each bird was then returned to its cage after the injection, and after 20 min (completing 2 h of food deprivation) the behavioural test of competition for food started.

Each bird cage was tested once a week, with an interval of 7 days between tests on the same cage to prevent possible carry over effects of the treatments. There were seven rounds of tests, thus lasting 7 weeks in total, and the order of the treatments differed among cages in a balanced manner, so that date is not a confounding factor in the experiment (calendar in Table A.1). In one of the seven rounds, all 4 birds (2 males and 2 females) of the same cage received

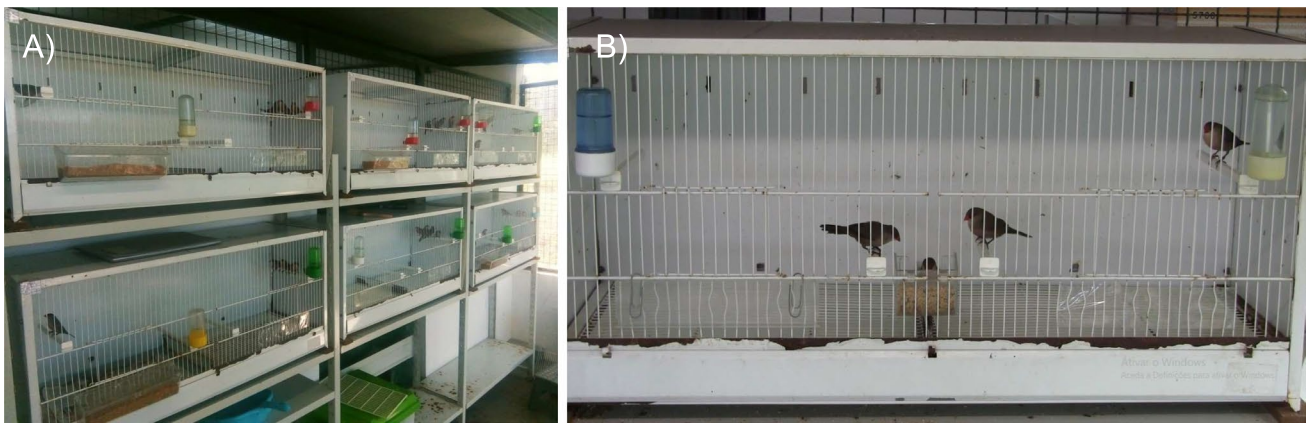

Fig. 1 Photographs from: **(A)** the six test cages, each containing 4 individuals (2 males and 2 females) and **(B)** an individual cage during a test of competition for food

control treatment (PBS). In the other six remaining rounds, one male and one female in the cage received PBS, and the other male and female of the same cage received an injection with either 8-OH-DPAT, fluoxetine or WAY 100,635. Each individual received the 8-OH-DPAT, fluoxetine and WAY 100,635 treatments only once (Table A.1). This happened in all the six birdcages. All treatments (control, 8-OH-DPAT, fluoxetine and WAY 100,635) were administered by intramuscular injection on the right side of the chest, in the pectoral muscle. The volume of the injections was 20 µl, administered with insulin syringes of 0.5 ml (29G). Dosages were based on previous studies (song sparrows (*Melospiza melodia morphna*): Sperry et al. 2003; wild cleaner wrasses (*Labroides dimidiatus)*: Paula et al. 2015), whose results indicated that the dosages were able to produce significant biological effects without causing harm to the individuals. These were as follow: 1 mg kg-1 of body mass of 5-HT_{1A} receptor agonist 8-OH-DPAT (H8520 Sigma-Aldrich, Darmstadt, Germany); 10 mg kg-1 of the selective 5-HT reuptake inhibitor (SSRI) fluoxetine (F132 Sigma-Aldrich); 1.5 mg kg-1 of the 5-HT_{1A} receptor antagonist WAY 100,635 (W108 Sigma-Aldrich). These were diluted in 20 µl of phosphate-buffered saline (PBS). Dosages were adjusted to the mean body weight of waxbills (9 g), which we measured before the onset of experiments. The control injections consisted only of 20 µl of PBS.

Competition for food test

We used a behavioural test involving the competition for food to assess social aggressiveness, following protocols developed earlier for the waxbills (Funghi et al. 2015, 2018). After 2 h of food deprivation, we placed a feeder attached to the front grid in the centre of the cage (Fig. 1), and video recorded the behaviour of the birds for 15 min with a video camera (Canon LEGRIA HF M306) placed on a grid wall ca. 1.5 m in front of the test cage. From the recorded videos, we quantified five behavioural variables (data in Table A.2), using separate focal observations for each of the four individuals in the cage: 1) total duration at the feeder: the total time, in seconds, that the focal individual spent on all its visits to the feeder. 2) latency to the feeder: the amount of time, in seconds, that the focal individual took to go to the feeder for the first time. 3) movements: the total number of changes in position between six different areas in the cage: each of the four perches, the feeder and the ground. Every movement to a different area, whether adjacent to the initial area or more distant, was counted as one movement, and movements within the same area were not counted. 4) allopreening: the total amount of time, in seconds, that an individual preened or groomed another individual. 5) aggressiveness: the total number of aggressive displays or attacks made by the focal individual (i.e., opening the beak towards another individual with stretched neck and spread wings, displacements, pecking, chasing). Behavioural quantification of the videos was always performed by the same observer (BCS), using The Observer XT 11 (Noldus Information Techonology b.v., Wageningen, the Netherlands) and blind to the experimental treatment (names of the video files were coded).

Statistical analysis

Since two of the behavioural measures (e.g., 'total duration at the feeder' and 'latency to the feeder') both relate to feeding and were correlated (-0.583, $p < 0.001$), we summarized them with a principal component analysis (PCA) from the correlation matrix. The first principal component (hereafter 'FeedingPC ') from this PCA explained 77.4% of variance and had a strong positive loading for 'Total duration at the feeder' (0.890) and a strong negative loading for 'Latency to the feeder' (-0.890). High scores indicate more time spent at the feeder and a lower latency to go there for the first time. The remaining behavioural variables were not strongly mutually correlated (all $|r| \leq 0.55$, using data from the control treatments; see Table A.3) and, since they refer to different behaviours and hypotheses, they were analysed separately. Inspection of histograms showed positively skewed distributions for 'allopreening' and 'aggressiveness', so they were $\log(x+1)$ transformed to approach normality. The variables 'movements' and 'FeedingPC' showed approximately normal distributions. Data for 'FeedingPC' can also be found in Table A.2.

We ran general linear mixed models (GLMMs), separately for each of the four behavioural variables ('FeedingPC', 'movements', 'allopreening' and 'aggressiveness') to test for within-individual differences between the control treatment and any of the serotonergic treatments, using the *lmer()* function in the R package "lme4" (v.1.1–23; Bates et al. 2014). In each GLMM, a behavioural trait was the dependent variable, treatment (control, 8-OH-DPAT, fluoxetine or WAY 100,635) was included as a fixed factor, cage identity was included as a random factor, to account for possible non-independence of data from within the same cage, and individual identity was included as a random factor nested within cages, to control for between-individual differences in behaviour. As controls, we only used the data from tests where all four individuals in a cage received PBS injection. We report the GLMM contrasts (i.e., the simple coefficients, without having run an ANOVA on the GLMM), which tests for differences between the reference level of the treatment (the control treatment) and each of the remaining levels (8-OH-DPAT, fluoxetine or WAY 100,635). We examined residuals using the command *check_model()* in the R package "performance" (v 0.7.0; Lüdecke et al. 2020), and in all models residuals were approximately normally distributed, homoscedastic and with homogeneous variance

in relation to fitted values. Since we tested three different compounds, we only consider an effect statistically significant when P is smaller than the Bonferroni-adjusted criterion for statistical of 0.05/3 = 0.017. All analyses were conducted in R v. 4.0.0 (R Core Team 2020). Since male and female waxbills had very similar responses to our experimental treatments (supplementary Fig. A.1) we report analyses for the two sexes together.

Results

Compared to the control treatment, treatment with the SSRI fluoxetine was associated with a lower FeedingPC score (i.e., longer latency to go to the feeder for the first time, and less time at the feeder; $t_{69} = -2.726$; p = 0.008, Fig. 2A; Table 1). FeedingPC scores when treated with 8-OH-DPAT or WAY 100,635 did not differ significantly from the control treatment (Table 1).

Treatment with the SSRI fluoxetine decreased movements compared to the control ($t_{69} = -3.428$; p = 0.001, Table 1, Fig. 2B). The number of movements when treated with 8-OH-DPAT or WAY 100,635 did not differ significantly from the control treatment (Table 1, Fig. 2B).

Compared to the control, fluoxetine significantly decreased aggressive behaviour ($t_{69} = -2.819$; p = 0.006, Table 1, Fig. 2C), while treatments with 8-OH-DPAT and WAY 100,635 did not change aggressive behaviour (Table 1, Fig. 2C). Finally, the amount of allopreening was not significantly affected by any of the treatments (Table 1, Fig. 2D).

Table 1 GLMM for the different behaviours analysed in the competition for food test

	β	SE	*t*	*P*
FeedingPC				
8-OH-DPAT	0.321	0.337	0.953	0.344
Fluoxetine	-0.919	0.337	-2.726	**0.008**
WAY 100,635	-0.36	0.337	-1.068	0.289
Sex	0.391	0.312	1.255	0.223
Movements				
8-OH-DPAT	16.625	9.663	1.721	0.09
Fluoxetine	-33.125	9.663	-3.428	**0.001**
WAY 100,635	-7.917	9.663	-0.819	0.415
sex	10.875	8.979	1.211	0.242
Aggressiveness				
8-OH-DPAT	0.229	0.347	0.661	0.511
Fluoxetine	-0.977	0.347	-2.819	**0.006**
WAY 100,635	-0.408	0.347	-1.176	0.244
sex	0.645	0.271	2.385	**0.029**
Allopreening				
8-OH-DPAT	-0.847	0.538	-1.575	0.120
Fluoxetine	0.089	0.538	0.166	0.869
WAY 100,635	-0.604	0.538	-1.124	0.265
sex	0.413	0.573	0.721	0.479

Note: Positive values of t indicate increases relative to the control treatment; negative values indicate decreases. Degrees of freedom are 141 except for the effect of sex, which are 22, and the total number of behavioural assays was 168. Significant P values are indicated in bold (the threshold for significance for the effects of treatments is 0.05 / 3 = 0.017)

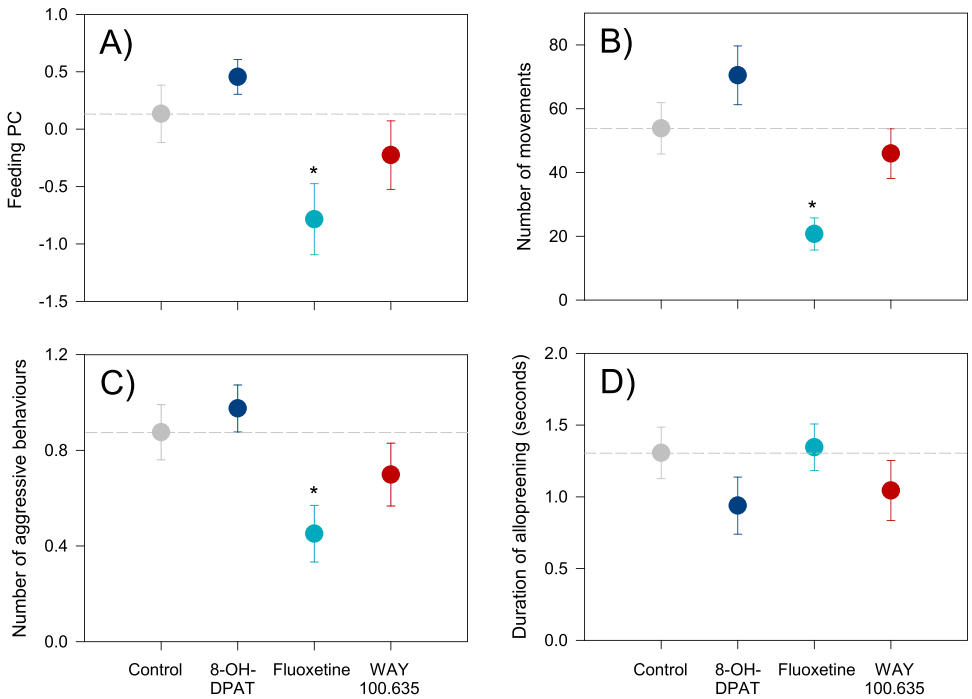

Fig. 2 Effects of the compounds tested comparatively to the control. **(A)** Feeding response (FeedingPC); **(B)** Movements; **(C)** Aggressiveness; **(D)** Duration of allopreening (in seconds). The mean and the standard error are represented for each. Significance is indicated as the contrast compared with the control treatment: * $P < 0.05/3 = 0.17$

Discussion

We tested if short term changes in 5-HT activity influenced waxbills aggression, feeding, movements and allopreening. As predicted, we found that treatment with fluoxetine, a selective 5-HT reuptake inhibitor (SSRI), resulted in an overall decrease of waxbill's aggressive behaviour, activity and feeding. However, treatment with 8-OH-DPAT, a selective 5-HT_{1A} receptor agonist, and WAY 100,635, a 5-HT_{1A} receptor antagonist, did not show discernible effects on waxbill behaviour. In what follows, we discuss serotonergic effects for the studied behaviours separately.

Fluoxetine-treated waxbills decreased activity levels compared to controls. Similar effects have been demonstrated in some fish species, in which short-term exposure to fluoxetine suppressed activity (Beulig and Fowler 2008; Kohlert et al. 2012; Barry 2013; Dzieweczynski et al. 2016). These instances of hypoactivity may be interpreted as anxiety-like behaviour because fluoxetine is not usually described as sedative. Anxiety is a secondary response to stress, which may take many forms, occurring when the stressor is absent or not clearly identified (reviewed in Fossat et al. 2014; Bacqué-Cazenave et al. 2020). In our case, perhaps the test of competition for food (including the food deprivation period and handling) is a stressor whose effect serotonin action may intensify. Several studies in fish and rodent species, have also reported anxiogenic-like effects following acute treatment with SSRIs (Griebel et al. 1994; Sánchez and Meier 1997; Maximino et al. 2013; Theodoridi et al. 2017). Acute rises in 5-HT can either increase (Griebel et al. 1994; Bagdy et al. 2001) or decrease (Inoue et al. 1996, 2004; Sánchez and Meier 1997) anxiety-like responses (Grillon et al. 2007), because 5-HT affects multiple brain structures that mediate anxiety via different pathways and receptors (Graeff et al. 1997; Grillon et al. 2007). Fluoxetine, as a SSRI, does not act specifically on receptors but rather on 5-HT overall availability, thus it may, in theory, interact with all 5-HT receptors (Shirayama et al. 1993; Sánchez and Meier 1997). For instance, Bagdy et al. (2001) suggested that the anxiogenic-like responses after a single dose of SSRIs, like fluoxetine, could be attributable to the activation of 5-HT_{2C} receptors in the amygdala (Westenberg and den Boer 1988; Griebel et al. 1994; Burghardt et al. 2004, 2007; Grillon et al. 2007) as the SSRI fluoxetine has been noted to be related with these receptor subtypes (Jenck et al. 1994; Pälvimäki et al. 1996; Bonhaus et al. 1997). Other studies support the affinity of the SSRI for the 5-HT_2 receptor family (Hyttel 1994; Sánchez and Meier 1997; Peng et al. 2014), implying that it acts as an antagonist for the 5-HT_{2C} receptors (Sánchez 1996; Sánchez and Meier 1997). Thus, our results might be attributable to pathways other than that involving the 5-HT_{1A} receptor, as the SSRI fluoxetine may also present high affinity for 5-HT_{2C} receptors. While at this point we cannot empirically demonstrate an influence of the 5-HT_{2C} pathways in waxbill activity levels, we may nonetheless suggest that this hypothesis merits future additional research. Perhaps this link between 5-HT shifts and anxiety response enhances animals' defence mechanisms, which may serve to protect them from numerous sources of dangers and inform other conspecifics of possible risks (Dickinson and Koenig 2018).

Unlike the case for the SSRI fluoxetine, we found that neither treatment with 8-OH-DPAT, a 5-HT_{1A} receptor agonist, nor with the antagonist WAY 100,635 affected movement. 5-HT can modulate activity in a rather complex manner, with similar dosages or similar exposure times sometimes exerting distinct behavioural responses (reviewed in Bacqué-Cazenave et al. 2020; Flaive et al. 2020), which may explain why in our results only some 5-HT pathways but not all affected movement. For instance, in rodents, the activation of the 5-HT_{1A} receptor usually produces anxiolytic-like effects (stimulate locomotor behaviour), depending on the site of injection and the type of 1A receptors being activated (Hillegaart and Hjorth 1989; Evenden and Ängeby-Möller 1990; Harrison and Markou 2001).

Regarding feeding behaviour, waxbills treated with the SSRI fluoxetine took longer to reach and spent less time at the feeder, similarly to previous results from studies in fish species (Gaworecki and Klaine 2008; Mennigen et al. 2010; Weinberger and Klaper 2014; Dzieweczynski et al. 2016). Similarly, to the results with movement, no other treatment (8-OH-DPAT and WAY 100,635) changed the feeding behaviour of waxbills. The absence of significant effects by WAY 100,635 on feeding response has been reported before, for example with pigeons (dos Santos et al. 2009).

In some species, treatment with 8-OH-DPAT decreased food intake (pigs: Ebenezer et al. 1999; chickens: Saadoun and Cabrera 2002), while it was also seen to increase food intake (pigeons: Steffens et al. 1997; dos Santos et al. 2015). 5-HT has been associated with an overall inhibitory effect of feeding (Denbow et al. 1982; Blundell 1984; Baranyiová 1990; Ebenezer et al. 1999; De Vry and Schreiber 2000; Saadoun and Cabrera 2002), but with little evidence for a relevant participation of the 5-HT_{1A} receptor (but see Reis and Marinho 2005, for effects on quails *Coturnix japonica*, and Mancilla-Diaz et al. 2005, for brain region-specific effects on rats *Rattus novergicus*), thus explaining the absence of effects in waxbills' feeding behaviour, for both the 5-HT_{1A} receptor agonist and antagonist (8-OH-DPAT and WAY 100,635, respectively).

None of our experimental treatments affected the amount of allopreening but increasing serotonergic availability with fluoxetine resulted in fewer aggressive

interactions. This latter result agrees with the meta-analysis of Carrillo et al. (2009), regarding the effects of pharmacological increases in 5-HT levels (with either SSRIs, 5-hydroxytryptophan, L-tryptophan, or 5-HT) on aggressive behaviour across vertebrates (birds, dogs, fish, hamsters, mice, rats, and monkeys), showing the overall inhibitory effect of higher levels of 5-HT on aggression. Since we found that fluoxetine also inhibited waxbill general activity and feeding, besides their aggressiveness, we cannot discard a general sedative effect of this drug in our birds. For example, in gerbils (*Meriones unguicalatus*), the effects of fluoxetine on social behaviour are influenced by previous housing conditions, with prosocial effects observed in individuals that were previously housed singly and sedative effects in individual previously maintained in groups (Hendrie et al. 2003). An alternative explanation is that fluoxetine produced anxiogenic effects, and in this way inhibited ongoing behaviours. In several species, acute SSRIs usually produce an anxiogenic-like effects in different behavioural paradigms (e.g., mouse: Mombereau et al. 2010; rat: Greenwood et al. 2008; fish: Maximino et al. 2013).

The inhibitory effect of acute fluoxetine on aggression has been most often attributed to the activation of both 5-HT_{1A} and 5-HT_{1B} autoreceptors, in several species (Piñeyro and Blier 1999; Sperry et al. 2003; Grillon et al. 2007; Beulig and Fowler 2008; Dennis et al. 2008; Gaworecki and Klaine 2008; Mennigen et al. 2010; Homberg 2012; Kohlert et al. 2012; Barry 2013), leading to a reduction of the firing rate of serotonergic neurons (Piñeyro and Blier 1999; Grillon et al. 2007; Homberg 2012), but also to its influence on the 5-HT_{2C} pathway (de Moura et al. 2022). The activation of 5-HT_{1A} receptors by treatment with a 5-HT_{1A} receptor agonist has been shown to decrease aggression in some species (hamsters: Joppa et al. 1997; song sparrows: Sperry et al. 2003; fighting fish: Clotfelter et al. 2007;), although there are also studies where it increased aggression (chickens: Dennis et al. 2008; cichlid fish: Stettler et al. 2021). Also, the 5-HT_{1A} receptor antagonist was shown to increase aggressiveness of treated bluestreak cleaner wrass females (*Labroides dimidiatus*) towards same-sex conspecifics (Paula et al. 2015), although other reports did not find similar effects (Sánchez 1997; Lopez-Mendoza et al. 1998; Bell et al. 1999; Clotfelter et al. 2007). In our experiments with waxbills, both 8-OH-DPAT and WAY 100,635 (5-HT_{1A} receptor agonist and antagonist, respectively) did not affect aggression. In general, the lack of an effect for both treatments could be due to species differences (i.e., no participation of the 5-HT_{1A} receptor on aggression in waxbills, 5-HT baseline levels), dose effects, or procedural differences.

In conclusion, fluoxetine treatment had a consistent effect in decreasing activity, feeding and aggressiveness in waxbills, producing an overall anxiogenic-like effect. No significant effects of 8-OH-DPAT and WAY 100,635 were found. Since 8-OH-DPAT and WAY 100,635 affect mainly 5-HT_{1A} receptor pathways, it is possible that the effects of fluoxetine that we found were due to its action on the 5-HT_{2C} receptor pathways instead. Our results may also be partially dependent on the dosage applied, resulting in hypoactivity under the effect of fluoxetine (Dagh 2013). Future studies should investigate potential effects when using different dosages, distinct time action frames, and other receptors that may also share a role in waxbills' aggressive-like response, specifically on 5-HT_{2C} receptor family.

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Data availability All data generated or analysed during this study are included in this published article (and its supplementary information files).

Declarations

Ethics approval All experimental protocols were approved by the ORBEA (Organism for Animal Welfare) of CIBIO-InBIO (ethics assessment # ORBEA_2019_Estrilda) and carried out in accordance with ARRIVE guidelines and regulations.

Conflict of interest The authors of the manuscript have no conflict of interest to declare.

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