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Quantity discrimination in angelfish, *Pterophyllum scalare*: a novel approach with food as the discriminant

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The ability to distinguish between different quantities of items is fundamental in many ecological contexts, and it has been shown in different animal species. This ability may also be context specific. Quantity estimation in fish has mainly been analysed in the context of social behaviour, whereas a majority of studies conducted with species other than fish tested it in the context of foraging. Surprisingly, little is known about the capacity of fish to discriminate between food quantities, possibly because of difficulties in testing individual fish in a novel, and thus aversive, test environment. Here, we present a novel approach that allowed us to test single angelfish, *Pterophyllum scalare*, while minimizing isolation-related stress. In binary choice tests, sets composed of similarly sized discrete food items differing in numerical size were presented and the spontaneous (untrained) choice of angelfish was investigated. In all contrasts tested in three experiments, angelfish preferred the numerically larger to the smaller food set. The performance of the fish was ratio dependent in the small but not in the large number range (more than four food items, contrasts that were investigated for the first time in fishes), and there was no significant difference in the magnitude of preference for the small versus the large values. However, overall results indicated that the response was ratio dependent, with an increase in accuracy as the numerical ratio between the contrasts increased. Furthermore, the same numerical ratios that were successfully discriminated with small quantities were also similarly discriminated with large quantities. Altogether, our results thus imply that angelfish utilize the approximate number system of quantity representation for the entire numerical range tested, and that their response is an attempt to maximize foraging success.

Quantity discrimination is a basic form of numerical competence. This ability allows individuals to choose between quantities that differ in the number of elements, and it has been shown in a range of animal species, including humans (e.g. see Lourenco, 2016; Vallortigara, 2015). Such capacity can provide fitness benefits in diverse ecological scenarios including intergroup conflicts (Bonanni, Natoli, Cafazzo, & Valsecchi, 2011), parental investment (Lyon, 2003) or predation risk contexts (Hager & Helfman, 1991). Most studies investigating quantity discrimination abilities have employed foraging situations, because in nature discrimination of the relative differences between food quantities available can directly affect survival rates. According to optimal foraging theory (Stephens & Krebs, 1986), when animals are faced with alternative foraging options, they should choose the one that provides the greatest net energetic gain. Therefore, the ability to assess different quantities is helpful to select the food source that provides the best payoff.

Most studies on quantity discrimination dealing with foraging decisions have been carried out in mammals and birds and under controlled laboratory conditions. This approach has allowed investigators to assess potential cognitive mechanisms underlying the discrimination. A variety of research methods have been adopted to investigate numerical abilities of animal species (reviewed in Agrillo & Bisazza, 2014), but a commonly adopted methodology to measure quantity discrimination involving foraging behaviour is the binary choice test. Under this paradigm, subjects have to select between two visible, simultaneously presented, numerically different sets of food items, which generally remain in view at the time of choice. This spontaneous quantity discrimination has been employed in studies with mammals

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(Baker, Morath, Rodzon, & Jordan, 2012; Bánszegi, Urrutia, Szenczi, & Hudson, 2016; Beran, Evans, & Harris, 2008; Cox & Montrose, 2016; Hanus & Call, 2007; Miletto Petrazzini & Wynne, 2016; Parrish, Evans, & Beran, 2015) and birds (Bogale, Aoyama, & Sugita, 2014; Garland, Low, & Burns, 2012; Rugani, Vallortigara, & Regolin, 2013), but it has also been utilized in other taxa such as amphibians (Krusche, Uller, & Dicke, 2010; Stancher, Rugani, Regolin, & Vallortigara, 2015; Uller, Jaeger, Guidry, & Martin, 2003) and reptiles (Miletto Petrazzini et al., 2017).

These studies have shown that animals are sensitive to quantitative differences in food sets, as most species studied were found to be able to discriminate between the item sets and showed significant preference for the larger quantity. Often, individuals have been subjected to discrimination tests that involve small (up to four) and large (more than four) quantities of food items, and sometimes discrimination ability has been found to be not uniform across these two number ranges. The results have suggested the existence of two distinct representational mechanisms: one to account for performance when numerically small sets are presented, and another when discrimination between numerically large sets was required. The latter system, named the approximate number system, was found to be imprecise. It adheres to Weber's law in that discrimination depends on the ratio, and not the absolute numerical difference, between the number of elements of the sets compared. In contrast, the mechanism proposed to operate with small quantities, named the object file system, is precise. It does not depend on the ratios between the two quantities but is limited to discrimination of elements in the small number range, that is, a maximum of three or four elements (Feigenson, Dehaene, & Spelke, 2004). Nevertheless, some evidence indicates the existence of only one system (the approximate number system) for the whole numerical range, as performance in some studies has been found to be dependent upon the numerical ratio in both the large and the small number range (Beran, 2004; Cantlon & Brannon, 2006; Perdue, Talbot, Stone, & Beran, 2012).

A growing number of studies have focused on the analysis of numerical cognition and quantitative abilities in fishes too (see Brown, 2015). Most of these studies have examined the discrimination between sets constituted by a different number of conspecifics, when the sets (shoals) are placed in each of the opposite sides of a test aquarium (see Agrillo, Miletto Petrazzini, & Bissazza, 2017). By transferring an individual test fish of a social species into a novel and potentially dangerous environment (the test aquarium), it was expected that, if the subject was able to distinguish between quantities of conspecifics, it should join the larger shoal as this offers better protection, diluting the potential predation risk for a solitary fish. In several fish species, a natural ability to assess quantities of conspecifics has been demonstrated (Agrillo, Dadda, & Serena, 2008; Buckingham, Wong, & Rosenthal, 2007; Piffer, Agrillo, & Hyde, 2012; Potrich, Sovrano, Stancher, & Vallortigara, 2015; Seguin & Gerlai, 2017; Stancher, Sovrano, Potrich, & Vallortigara, 2013; Thünken, Eigster, & Frommen, 2014). As in other vertebrates, a controversy exists, however, over the representational mechanism(s) underlying discrimination in fishes. Some of the studies support the existence of two distinct mechanisms (Agrillo, Miletto Petrazzini, & Bisazza, 2014; Agrillo, Piffer, Bisazza, & Butterworth, 2012; Piffer et al., 2012), whereas other studies support the idea of a single mechanism operating over the entire numerical range (Mehlis, Thünken, Bakker, & Frommen, 2015; Miletto Petrazzini & Agrillo, 2016; Potrich et al., 2015).

In contrast with other animal species, however, only a very few studies in fish have used food as the discriminative stimulus, and the focus on foraging behaviour in this type of test has only begun recently. Difficulties of testing an individual fish in a novel, potentially frightening environment, together with complications arising from presenting food in water, including odour cues, may account for the lack of food quantity discrimination studies in fish. In fact, in the only two studies published to date, each individual fish had to be acclimatized to the novel environment (the test aquarium) for a week, and smaller conspecifics were also introduced to reduce the potential effects of individual housing as well as to facilitate adaptation and response to the food stimulus (Lucon-Xiccato & Dadda, 2017; Lucon-Xiccato, Miletto Petrazzini, Agrillo, & Bisazza, 2015). These studies, conducted with guppies, *Poecilia reticulata*, tested only a few contrasts of sets of similarly sized food items. Lucon-Xiccato et al. (2015) reported that the guppies were able to distinguish between different numbers of food items up to a 2:1 ratio (4 versus 1 and 4 versus 2 items), but not between smaller ratios (number of elements in the larger set divided by the number of elements in the smaller set). For example, they were unable to discriminate between 6 versus 4 sets of discrete food items (Lucon-Xiccato & Dadda, 2017). However, no study has examined the abilities of fish to discriminate between food quantities in the large versus the small number range using multiple contrasts systematically varied.

The angelfish, *Pterophyllum scalare*, has been used in the analysis of quantity discrimination abilities. These fish have been shown to spontaneously discriminate shoals of conspecifics differing in numerical size when the contrasted shoals were in the large number range, when they were in the small number range and when one of the contrasted shoals belonged to the large and the other to the small number range (Gómez-Laplaza & Gerlai, 2011a, 2011b, 2015, 2016a, 2016b). Furthermore, in addition to being able to show significant preference for the larger shoal when both contrasted shoals were simultaneously visible, angelfish were also found to be able to remember where the larger shoal used to be shown, a result that demonstrated mental representation (memory) of different quantities of items in this small teleost (Gómez-Laplaza, Caicoya, & Gerlai, 2017). However, quantity discrimination abilities of angelfish in contexts other than social has not been investigated, although two studies have used training procedures with food as reward (Agrillo, Miletto Petrazzini, Tagliapietra, & Bisazza, 2012; Miletto Petrazzini, Agrillo, Izard, & Bisazza, 2016). It is possible that natural selection shaped discrimination abilities for quantities of shoals and for quantities of food items differently. If performance is context specific (Miletto Petrazzini, Agrillo, Piffer, & Bisazza, 2014), a different ecological context employed experimentally may reveal different, previously unknown, numerical cognitive features of angelfish. The goal of the current study was to explore this possibility, and to investigate discrimination ability of angelfish when the items to be discriminated were food. In chicks, *Gallus gallus domesticus*, for example, the response was not found to be context specific, that is, preference for the numerically large quantity was found when discriminating between both numerically distinct social partners and food quantities. The discrimination response to social attractors, however, was found to be better than that to food attractors (Rugani, Cavazzana, Vallortigara, & Regolin, 2013).

In the present study, we investigated the spontaneous ability of angelfish to discriminate between food quantities using a two-choice discrimination task between sets composed of discrete homogeneously sized food items differing only in numerical size. Initially, we employed the same procedure we previously utilized for the analysis of discrimination between shoals of conspecifics. This procedure required individual housing and testing of the subjects (which motivated them to choose conspecifics). The