Animal Behaviour 112 (2016) 29–37

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Discrimination of large quantities: Weber's law and short-term memory in angelfish, *Pterophyllum scalare*

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ARTICLE INFO

Article history:
Received 11 July 2015
Initial acceptance 2 September 2015
Final acceptance 6 October 2015
Available online
MS. number: 15-00601

Keywords:
analogue magnitude system
angelfish
large numbers
numerical cognition
quantity discrimination
short-term memory
Weber's law

The ability to discriminate between different quantities has important ecological relevance for animals when engaging in behaviours such as forming groups, foraging or trying to avoid predators. Quantity discrimination has been shown in a diversity of human and nonhuman animal species. In angelfish this discrimination ability has been investigated using dichotomous choice tests when the numerically different stimulus groups (shoals) of conspecifics were fully visible to the test fish. Here, using a new procedure we investigated whether test fish were able to discriminate between the contrasting shoals using their memory. After a period of full visual access to the contrasted shoals on the two sides of their test tank, the test fish was required to make a choice while being able to see only a single member of the stimulus shoals on each side. With this cognitively more demanding procedure we tested discrimination between numerically large shoals (≥ four fish per stimulus shoal). As in our previous studies, we found that angelfish consistently chose the larger of the two shoals when the shoals differed by a 2:1 or higher ratio, but not those that differed by a 3:2 or 4:3 ratio. The results followed Weber's law in that performance became poorer as the ratio between the two stimulus shoals approached one. In addition, when we kept the absolute difference between the contrasted shoals constant, discrimination was less accurate as the shoal sizes increased. This pattern of results lends support for the analogue magnitude representational system in the angelfish, a nonverbal approximation system believed to be employed by a diversity of human and nonhuman animal species. Furthermore, our results also demonstrate that angelfish remember the different shoals presented to them, i.e. they make their choice based upon mental representation of the different quantities.

Comparative studies have demonstrated that human infants and nonhuman animals share an ability to discriminate between numerical quantities. These studies also suggest similarities in the cognitive processes of a variety of species in assessing which set contains more elements (see Feigenson, Dehaene, & Spelke, 2004). Notably, these processes may be dependent upon the number of elements in the sets. For small sets (up to three or four elements) the process involves distinguishing individual elements and tracking these elements via 'object files'. This system is limited to only a few items per set due to capacity constraints of working memory and/or to attentional limits (e.g. Burr, Turi, & Anobile, 2010; Hyde, 2011). Under this system the comparison between sets fails when the numerical limit is surpassed.

For large sets (more than three or four elements) quantity discrimination appears to be supported by an approximate estimation system that allows the representation of the quantity of a set in an analogue manner, with representations becoming increasingly imprecise as quantities increase (Dehaene, 2009). This ability appears not to be dependent on the absolute difference between the quantities, but rather on the ratio between them (Feigenson et al., 2004). Thus, unlike an object file system, discrimination of large quantities follows Weber's law: as the ratio of the larger set to the smaller set approaches one, discrimination becomes increasingly difficult whereas as the ratio increases, discrimination becomes easier (Gallistel & Gelman, 2000).

Most evidence of the existence of these two systems comes from studies on preverbal human infants. Using a variety of experimental approaches infants have been shown to be able to discriminate between quantities ranging from one to three, but fail to discriminate between sets that cross the large/small boundary, such as four versus three, four versus two, four versus one (Feigenson & Carey,

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http://dx.doi.org/10.1016/j.anbehav.2015.10.022
0003-3472/

2003, 2005; Lipton & Spelke, 2004; Xu, 2003). However, infants are able to discriminate between sets when both sets contain four or more items and the numerical difference between the size of the sets increases (Feigenson et al., 2004; Lipton & Spelke, 2004; Xu, 2003; Xu & Spelke, 2000; Xu, Spelke, & Goddard, 2005; see also Cordes & Brannon, 2008). Similar results have been found in some nonhuman animal species (Agrillo, Dadda, & Bisazza, 2007; Agrillo, Piffer, Bisazza, & Butterworth, 2012; Hunt, Low, & Burns, 2008; Mehlis, Thünken, Bakker, & Frommen, 2015; Piffer, Agrillo, & Hyde, 2012; Rugani, Regolin, & Vallortigara, 2008; Tomonaga & Matsuzawa, 2002; Uller & Lewis, 2009).

Evidence from other studies, however, indicates that discrimination of both small and large sets may be supported by the same approximate number system (e.g. Cantlon & Brannon, 2006). The idea that the approximate number system operates over the entire range of numbers is mostly based on results obtained with nonhuman primates (Barnard et al., 2013; Beran, 2004, 2007; Hanus & Call, 2007; Jones & Brannon, 2012; Judge, Evans, & Vyas, 2005). Recent evidence with canids (Baker, Morath, Rodzon, & Jordan, 2012) and avian species also contrasts with the idea of two separate systems (Pepperberg, 2012; Rugani, Cavazzana, Vallortigara, & Regolin, 2013; Rugani, Vallortigara, & Regolin, 2014; Ujfalussy, Miklósi, Bugnyar, & Kotrschal, 2014), and some results in fish also appear to support this notion (Bisazza, Tagliapietra, Bertolucci, Foà, & Agrillo, 2014; Mehlis et al., 2015; Miletto Petrazzini & Agrillo, 2015; Stancher, Sovrano, Potrich, & Vallortigara, 2013).

An intense debate continues over the presence of one versus two processing systems in representing small numbers/quantities. However, a large body of empirical evidence indicates that the discrimination of large quantities relies on analogue magnitude representations (i.e. is ratio dependent; see Beran, 2008; Brannon, 2006). One typical behavioural signature of this system is that the smaller the numerical difference between the sets, the poorer the performance becomes (the distance effect). Another typical signature is that when the distance is held constant, the larger the set size, the harder the discrimination (the numerical size or magnitude effect). These effects correspond to Weber's law (Gallistel & Gelman, 2000).

Using a training procedure with food as reward, the angelfish *Pterophyllum scalare* has been shown to be able to discriminate between two sets of geometrical figures differing in numerical size (Agrillo, Miletto Petrazzini, Tagliapietra, & Bisazza, 2012). Our previous studies with angelfish have also demonstrated that this cichlid species possesses cognitive abilities to spontaneously (i.e. in the absence of specific training) discriminate between shoals (groups) of conspecifics that differ in the number of members. These capabilities were shown when the contrasting shoals consisted of both a relatively large number of members or ratios $\geq$1.8:1 (e.g. 12 versus three, nine versus three, eight versus four, nine versus five, Gómez-Laplaza & Gerlai, 2011a) and a small number of members (e.g. three versus one, two versus one, three versus two, Gómez-Laplaza & Gerlai, 2011b). With large numbers, the discrimination decisions appeared to follow Weber's law: as the relative shoal sizes became more similar, the discrimination was more difficult. In these studies we used binary choice tests and during testing the stimulus shoals were fully visible to the subjects.

Another approach utilized in the analysis of quantity discrimination of a variety of animal species including human infants (e.g. Feigenson & Carey, 2005; Feigenson, Carey, & Hauser, 2002) employs occlusion of the contrasted stimulus sets in such a way that they are not visible at the moment of choice (reviewed in Agrillo & Bisazza, 2014). In this task the subject must be able to use mental representations (i.e. memory) of the quantities previously seen.

Recently, we have developed a new approach for angelfish (Gómez-Laplaza & Gerlai, 2015) that utilizes this principle. In this task, the stimuli are not fully visible at the moment of choice, and full continuous cues of the shoals are unavailable. The procedure consists of presenting numerically different shoals of conspecifics at the opposite ends of a test aquarium and in full view of the test fish during a pretest period. During the subsequent test phase all but one stimulus fish of each of the two contrasted shoals are hidden from view, and the test fish is required to make a choice based upon memory of the previous shoal presentation. By employing this new procedure, a modification of that employed by Stancher et al. (2013) in redtail splitfin, *Xenotoca eiseni*, we investigated whether angelfish could rely on their working memory of the location of the contrasted shoals. Although the retention interval was very short (2 s) and thus the working memory demand was not high, our results showed that angelfish were able to remember the prior location of numerically different shoals when the shoal sizes were small (Gómez-Laplaza & Gerlai, 2015). Under these conditions, angelfish showed a significant preference for the zone close to the larger stimulus shoals when the contrasts consisted of four versus one, three versus one, two versus one, three versus two and four versus two. However, angelfish did not show discrimination when the contrasts were of four versus three, five versus four and six versus four and, as mentioned above, at the time of choice only one stimulus fish of each stimulus shoal was visible to the test fish.

The aim of the present study was to investigate whether angelfish are able to discriminate large shoals of conspecifics (composed of four or more members) using their memory. First we tested the response of experimental fish to pairs of large shoals differing in numerical ratio in order to assess whether the performance of angelfish conforms to the signatures of the analogue magnitude system, and whether memory plays a role in the discrimination. To further investigate the importance of memory, we increased the retention interval during which the shoals were completely occluded from 2 s to 15 s, thus breaking any visual contact with both shoals, before allowing only one angelfish of each stimulus shoal to be visible to the subjects during testing.

GENERAL METHODS

Ethical Note

Wild-type juvenile angelfish (3.0–3.3 cm standard length) were obtained from local commercial suppliers. The experiments described here comply with the current law of the country (Spain) in which they were performed and the permit to conduct the study was obtained from the Ethics Committee of the University of Oviedo (permit ref.: 13-INV-2010). Essentially, the experiments involved behavioural observations with as little intervention by the observer as possible. Fish were gently transferred between tanks in small Perspex containers filled with water from their own aquarium, a procedure that minimized handling-induced stress. All fish were kept under optimal conditions and remained healthy during the experiments, and were returned to the suppliers at the end of the study.

Subjects and Housing Conditions

As angelfish are sexually monomorphic, we studied only juvenile fish so as to eliminate possible confounding effects arising from courtship or agonistic/territorial interactions. The fish were housed in glass holding aquaria (60 $\times$ 30 cm and 40 cm deep) in groups of 24–26 and were allowed a minimum of a 2-week acclimation period before behavioural testing.