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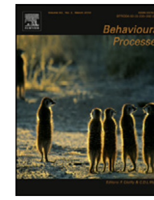

Relative quantity judgments in the beluga whale (*Delphinapterus leucas*) and the bottlenose dolphin (*Tursiops truncatus*)

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ABSTRACT

Numerous studies have documented the ability of many species to make relative quantity judgments using an analogue magnitude system. We investigated whether one beluga whale, *Delphinapterus leucas*, and three bottlenose dolphins, *Tursiops truncatus*, were capable of selecting the larger of two sets of quantities, and analyzed if their performance matched predictions from the object file model versus the analog accumulator model. In Experiment 1, the two sets were presented simultaneously, under water, and they were visually (condition 1) or echoically (condition 2) available at the time of choice. In experiment 2, the two sets were presented above the water, successively (condition 1) or sequentially, item-by-item (condition 2), so that they were not visually available at the time of choice (condition 1) or at any time throughout the experiment (condition 2). We analyzed the effect of the ratio between quantities, the difference between quantities, and the total number of items presented on the subjects' choices. All subjects selected the larger of the two sets of quantities above chance levels in all conditions. However, unlike most previous studies, the subjects' choices did not match the predictions from the accumulator model. Whether these findings reflect interspecies differences in the mechanisms which underpin relative quantity judgments remains to be determined.

1. General introduction

Numerical cognition stands at the core of unique human cognitive achievements but its evolutionary origins and precursors remain to be established (Uller, 2008). The ability to assess relative quantities is of adaptive value to deal with some of the ecological and social challenges that many animal species encounter in their lives (Shettleworth, 2010). Accordingly, there is growing evidence of rudimentary numerical competence in numerous non-human species (great apes: Anderson et al., 2005; Beran et al., 2005; Boysen and Berntson, 1989; Call, 2000; Dooley and Gill, 1977; Hanus and Call, 2007; Rumbaugh et al., 1987; Silberberg and Fujita, 1996; monkeys: Anderson et al., 2000; Beran, 2007a,b; Hauser et al., 2000; lions: McComb et al., 1994; raccoons: Davis, 1984; rats: Davis et al., 1989; dogs: Bonanni et al., 2011; Ward and Smuts, 2007; sea lions: Abramson et al., 2011; elephants: Irie-Sugimoto et al., 2009; horses: Uller and Lewis, 2009; crows: Smirnova et al., 2000; parrots: Pepperberg, 1987, 2006; pigeons: Alsop and Honig, 1991; chicks: Rugani et al., 2007; amphibians: Uller et al., 2003; fishes: Agrillo et al., 2007; Gòmez-Laplaza and Gerlai, 2011; insects: Carazo et al., 2009). These findings suggest that human numerical skills might build on an evolutionarily ancestral capacity, a language-independent representation of numbers, that supports elementary arithmetic computations and that is somehow shared by nonverbal animals (for overviews see Brannon and Terrace, 2002; Butterworth, 1999; Cantlon, 2012; Dehaene, 1997; Gallistel, 1990; Matsuzawa, 2009; Uller, 2008).

Several mechanisms have been proposed to account for this competence. Early proposals included perceptual mechanisms such as subitizing (Davis and Perusse, 1988) or prototype matching (Thomas, 1992). However, neither can account for some of the evidence currently available, for example, when individuals discriminate between quantities that fall outside the subitizing range (Dooley and Gill, 1977), or when they discriminate between sets that are presented sequentially or item-by-item (Beran, 2001; Call,

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200; Hanus and Call, 2007; Irie-Sugimoto et al., 2009). In fact, the ability to solve the latter condition requires a mental comparison mechanism that goes beyond a merely perceptual one. This non-perceptual mechanism can take two forms, namely, the object file model, which is a digital mechanism (Kahneman and Treisman, 1984; Kahneman et al., 1992; Simon et al., 1995; Uller et al., 1999), and the accumulator model, which is an analog mechanism (Dehaene, 1997; Gallistel and Gelman, 2000; Meck and Church, 1983; Wynn, 1998).

Although most would agree that both kinds of representations could be used in numerical reasoning, there is no agreement about its extent (Dehaene, 2001; Carey, 2001; Wiese, 2003). According to the object file model, numerical capacity works on mental (symbolic) representations of a set of visual objects, i.e., the object files. Each object file is a mental token that represents each element of a set of elements, yielding exactly as many files (mental tokens) as objects that are filed in short-term memory (Uller et al., 1999; Wiese, 2003). In making relative quantity judgments, the subject would create one object file for each item presented in a set, and would thus produce a one-to-one correspondence between "active" object files and the number of presented items (Hauser and Carey, 1998). Quantitative differences between two arrays are detected by comparing the two representations. In contrast, according to the accumulator model, animals cannot discriminate absolute numbers or label each separate object; instead they recognize quantities by means of an accumulated analog representation, the accumulation of continuous quantities in proportion to the number of quantified elements (Meck and Church, 1983). That is, discrete quantities can be represented as mental magnitudes that could be seen as an analog of the perceived discrete quantities. In making relative quantity judgments, the animal would have two noisy analog representations of the two sets. The extent to which these two fuzzy representations overlap would determine the likelihood of confusion about their relative magnitude.

Although the object file model does provide an accurate representation of quantities, it is, however, limited to small quantities, because a mechanism like this requires memory space, which implies a limited capacity of processing quantities greater than 3 or 4 due to limitations for processing stimulus items that are perceptually available simultaneously (Uller et al., 1999). By contrast, although the analog magnitude representation of the accumulator model is rather fuzzy (Gallistel and Gelman, 2000), as the accuracy of discrimination decreases with increasing quantities (when the absolute differences are kept constant), it can, however, deal with larger sets, since it has no a priori limit (Dehaene, 2001; Gallistel and Gelman, 2000).

The vast majority of studies on relative quantities support the accumulator model rather than the object file model because they have reported performance that is ratio-dependent with no clear-cut drop out beyond certain quantities. In fact, there are only three studies (all in rhesus macaques) that have found some evidence in favor of the object file model (Hauser and Carey, 2003; Hauser et al., 2000; Wood et al., 2008). However, Beran (2007a,b) also tested the same species finding no support for the object file model. Interestingly, Irie-Sugimoto et al. (2009) found that Asian elephants consistently selected the larger of two quantities but found neither a ratio-dependent performance nor a clear-cut drop out beyond certain quantities. Irie-Sugimoto et al. (2009) suggested that Asian elephants by virtue of their memory capacity may possess a 'large object-file model'. Note, however, that African elephants, unlike their Asian counterparts, do show ratio-dependent performance, which is consistent with the accumulator model (Irie, 2012; Perdue et al., 2012). The putative difference between these two closely related species is intriguing and deserves further comparative scrutiny.

Cetacean odontocetes might be a particularly interesting group on which to investigate numerical abilities given the peculiarities of their socio-ecology and neurobiology compared with most terrestrial mammals. Bottlenose dolphins *(Tursiops truncatus)* can learn to choose the object with the greatest fish value (Mitchell et al., 1985) and are capable of representing ordinal relations among numerosities (Jaakkola et al., 2005; Killian et al., 2003). It has been proposed that dolphins' quantity representation is supported by an analog magnitude mechanism (Jaakkola et al., 2005).

However, it is unknown whether bottlenose dolphins would also be able to choose the largest of two quantities when they are not perceptually available at the time of choice. Recall that quantities in previous studies with dolphins were always perceptually available at the time of choice. Moreover, as far as we know, no studies have investigated the quantitative abilities of other odontocetes. Beluga whales (*Delphinapterus leucas*), in particular, may demonstrate cognitive abilities comparable to those of bottlenose dolphins given that they also possess large brains, live in sophisticated social systems, and are highly trainable (Brodie, 1989; Defran and Pryor, 1980; Samuels and Tyack, 2000; Nowak, 1991).

In the present study, we investigated the ability of one beluga and three bottlenose dolphins to compare and operate on quantities of food items. We wanted to determine whether, in the absence of training, subjects were able to (1) select the larger of two sets of quantities, (2) using both visual cues or echolocation, (3) when the quantities were not perceptually available at the time of choice, (4) for a range of quantities that allowed us to characterize the representational system underpinning their responses. To address these questions, we tested four different conditions in two experiments. In experiment 1 the two sets of quantities were presented simultaneously as whole sets, that is, the subjects could compare the two sets directly (e.g., Call, 2000; Hanus and Call, 2007; Irie-Sugimoto et al., 2009). In condition 1, the two sets were presented visually, whereas in condition 2 the two sets were presented in opaque boxes, that is, to pass the test, the subject had to use echolocation. In experiment 2, the two sets of quantities were presented successively (condition 1) or sequentially, item-by-item (condition 2), so that the totality of items were perceptually unavailable at the time of choice (condition 1) or at any time throughout the task (condition 2) (Beran, 2001; Call, 2000; Hanus and Call, 2007; Irie-Sugimoto et al., 2009). Thus, to succeed in the two conditions of experiment 2, subjects were required to store and compare the quantities mentally. Finally, to explore the nature of the mental mechanism underlying the quantitative cognition of the subjects, we analyzed, for each type of presentation, the effect of the ratio between quantities, the difference between quantities, and the total number of items presented. A predominant influence of the ratio between quantities on the subject's performance (less accurate discrimination as the ratio between quantities increases) would support an analog representational mechanism, as suggested by the accumulator model. In contrast, the object-file model predicts a cut-off point in discrimination ability when quantities exceed the number of four.

2. General methods

2.1. Subjects and general procedure

We tested one female beluga whale (*D. leucas*) housed at L'Oceanografic Aquarium in Valencia, Spain, and three female bottlenose dolphins (*T. truncatus*), two of which were housed at Marineland Aquarium in Antibes, France, and one was housed at Madrid Zoo Aquarium, in Spain (Table 1).

The beluga whale (Y) was mother-reared and captured when she was 1-year-old in the Okhotsk Sea. She had been housed at