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A sense of number in invertebrates

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ABSTRACT

Non-symbolic numerical abilities are widespread among vertebrates due to their important adaptive value. Moreover, these abilities were considered peculiar of vertebrate species as numerical competence is regarded as cognitively sophisticated. However, recent evidence convincingly showed that this is not the case: invertebrates, with their limited number of neurons, proved able to successfully discriminate different quantities (e.g., of prey), to use the ordinal property of numbers, to solve arithmetic operations as addition and subtraction and even to master the concept of zero numerosity. To date, though, the debate is still open on the presence and the nature of a «sense of number» in invertebrates. Whether this is peculiar for discrete countable quantities (numerosities) or whether this is part of a more general magnitude system dealing with both discrete and continuous quantities, as hypothesized for humans and other vertebrates. Here we reviewed the main studies on numerical abilities of invertebrates, discussing in particular the recent findings supporting the hypothesis of a general mechanism that allows for processing of both discrete (i.e., number) and continuous dimensions (e.g., space).

1. Introduction

The non-symbolic and non-verbal type of cognitive ability of dealing with the numerical value of an array has been documented in the majority of animal species, both vertebrate and invertebrate. It is though not any longer considered a prerogative of human beings (see e.g. for some recent reviews [1–6]). The ability to process numerical information was, for a long time, thought to be linked to language, but several studies demonstrated the existence of differential neuronal patterns in participants involved in lingual *vs.* numerical tasks [7]. Developmental research also demonstrated that numerical cognition is present already in newborns and infants, suggesting the existence of numerical abilities at a prelinguistic stage of development [8–10], as well as in human traditional societies with a restricted abstract vocabulary [11,12].

Discrimination of numerosities appears highly adaptive (see e.g. Ref. [13,14]). Animals can use their “sense of number” to make choices that enhance their chance of survival, e.g., avoiding predation risks [15–18], maximizing foraging intake or hunting success [19–22], succeeding in intergroup conflicts [23–28], increasing their mating opportunities [29], maintaining the social contact with the larger group of conspecifics [30], and reducing brood parasitism [31]. It has also been argued that their ability to discriminate different numerical items seems to be in place at birth, as in the case of domestic chicks [32,33].

These abilities would be supported by a non-verbal *number sense* or *Approximate Number System (ANS),* which has been described as an innate capacity to process numerosity [1,5,34–36]. The ANS allows estimation and discrimination of discrete quantities with an accuracy which depends on the numerical ratio of the comparison (e.g., discrimination of 5 *vs.* 10 items is easier than discrimination of 10 *vs.* 15 items; [37]), obeying to Weber’s Law (i.e., the just noticeable difference between two elements depends on the ratio between their magnitudes, rather than their absolute difference; see Ref. [36]). The *numerical distance* effect and the *numerical size* effect represent the basic key signatures of the ANS system. The *numerical distance* effect describes the increasing accuracy in the ability to discriminate between two quantities when

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their numerical distance increases (e.g., to discriminate 6 *vs.* 9 is easier than to discriminate 6 *vs.* 7; [2]). The *numerical size* effect describes the decrease in accuracy in discriminating larger quantities with equal numerical distance (e.g., it is easier to discriminate 5 *vs.* 6 items than 10 *vs.* 11 items, in spite of the numerical distance being the same; [2]).

Nowadays, we are fully aware of the ability of humans and other animals to use numerical information to deal with cognitive tasks, both in ecological and laboratory settings. However, some behavioral [38] and neurobiological [39] evidence also support the view that the ability to deal with numerosities would be part of a more general system dealing with quantity (or magnitude), underlying the ability of processing also continuous dimensions e.g. space and time. Gallistel (1989) was the first to suggest the existence of a «common mental currency » that would enable the representation of discrete (e.g., numbers) and continuous (e.g., space and time) dimensions in the brain [40]. Later evidence from behavioral and brain studies demonstrated the existence of mutual associations between number and time [41], number and space [42], and space and time [43,44] in humans and other animal species. Walsh (2003) also proposed *A Theory Of Magnitude* (ATOM) suggesting that a common prelinguistic framework would allow organisms the encoding of different "prothetic dimensions" (i.e., dimensions that can be "more than" or "less than"), such as numbers, space, time, brightness or length [45]. According to the ATOM theory, the simultaneous processing of different magnitudes would lead to symmetrical interference across dimensions, as in the case of studies with human infants that process similarly numerical, temporal, and spatial dimensions [46]. In their study, Merritt and colleagues (2010) compared the interaction between space and time in human adults and monkeys. Subjects had to judge either the length or the temporal duration of a line presented on a computer screen. At test, they were faced with lines having a different combination of features (e.g., longer length and shorter temporal duration and vice versa). The results showed a prevalent interference of the spatial over the temporal dimension in humans, while monkeys showed a mutual interference of the two magnitudes, without a significantly larger effect of spatial over temporal information [38]. An association between space and time is also found in pigeons [44], providing further support to the hypothesis that a general system for magnitude representations is observed even in non-mammals.

2. Numerical abilities of invertebrates

For a long time, invertebrates have been virtually neglected in the study of cognitive abilities, and chiefly so for what concerns numerical cognition, mainly due to their smaller brains [47] and different behavioral, anatomical and ecological traits [48]. Notwithstanding, several studies have now clearly demonstrated that information based on numerosity can provide an advantage in terms of fitness also to invertebrates [49] (Fig. 1).

Numbers have an important adaptive value for all animals, likewise, several species of invertebrates rely on numbers to make more sensible choices. For example, mealworm beetles use numerical information during mating by choosing the substrate bearing odors of the larger number of females [50,51]. Honeybees and ants use proto-counting during navigation [52–55]. Bumblebees and solitary bees, spiders and ladybirds assess the number of competitors or the number of food sources during foraging and hunting activities [56–60]. Last but not least, ants are more likely to increase their aggressive behavior if they are part of a large group, rather than when they are alone [61].

The numerical abilities of invertebrates have been assessed using a variety of methods, including spontaneous preferences and associative learning, overall providing quite convincing evidence of the presence of a *number sense* in invertebrates. For instance, cuttlefish show a spontaneous preference for the larger food amount when presented with 1 *vs.* 2, 2 *vs.* 3, 3 *vs.* 4, and 4 *vs.* 5 shrimps in a two-alternative choice [62]. The same preference was also observed when cuttlefish were presented with numerical fractions, i.e., non-integer numbers such as 1 *vs.* 1.5, 1.5 *vs.* 2, and 2 *vs.* 2.5 [63]. Among insects, foraging honeybees showed a preference for the visual array containing the larger quantity of items. Free-flying foragers underwent a priming phase where a single yellow disk associated with a drop of sucrose solution was presented. This step allowed the simple association between stimuli (i.e., the yellow disk and food) without providing any numerical information. During the probe test phase, bees were presented with thirteen different novel numerical comparisons ranging from 0.08 to 0.8 ratio difference (i.e., 1 *vs.* 2, 1 *vs.* 3, 1 *vs.* 4, 1 *vs.* 12, 2 *vs.* 3, 2 *vs.* 4, 3 *vs.* 4, 4 *vs.* 5, 4 *vs.* 6, 4 *vs.* 7, 4 *vs.* 8, 4 *vs.* 12, 4 *vs.* 20). Honeybees showed a spontaneous preference for the larger number of elements when the smaller numerosity was "1" and the magnitude difference between quantities was sufficiently high (e.g., 1 *vs.* 12, 1 *vs.* 4 and 1 *vs.* 3; [64]).

Insects, in particular, proved to have impressive learning abilities associated with numbers, and to be able to successfully learn to associate numerical quantities with appetitive rewards [65,66]. In a study, MaBouDi and colleagues (2020) trained four groups of bumblebees to choose either the smaller or the larger quantity in a 1 *vs.* 3 or 2 *vs.* 4 contrast (i.e., yellow dots or stars). Bees underwent unrewarded (in extinction) test trials to assess their ability to transfer the numerical learning to novel shapes (e.g., cross), colors (e.g., purple), and numerical contrasts (i.e., bees trained to discriminate 1 *vs.* 3 elements were tested with 2 *vs.* 4 numerical contrast and vice versa). The results showed that bees were selectively able to rely on numerical information to solve the discrimination when the elements had different visual properties (shape and color). Moreover, bees transferred the numerical relations "smaller than" and "larger than" learned during the training, to novel numerical comparisons (e.g., bees trained to choose 1 over 3 items, were more likely to select 2 over 4 items in the test phase; [67]). Honeybees were also shown to be able to successfully choose the correct numerosity in delayed match-to-sample tasks [66]. Interestingly, in these tasks bees appeared to spontaneously rely on an absolute numerical value (i.e., selecting the array containing a specific number of items) over a more general relative numerical value (i.e., selecting the smaller/larger array regardless of the number of items contained [68]).

Insects are also able to deal with ordinal (other than cardinal) aspect of numerosity. Chittka and collaborators (1995) trained honeybee foragers to collect food from a feeder placed between the third and the fourth of a line of identical tents. To test their ability to "count" the number of landmarks *en route* at test, the distance of the tents was manipulated, creating a contrast between number of landmarks and flying distance. A significant portion of honeybees (22%) landed on the feeder that was placed between the third and the fourth tent, showing to be able to take into account the ordered number of landmarks to locate the food source [52]. Similar results were obtained in experiments in which bees were trained to fly into a tunnel and pass a fixed number of landmarks (i.e., stripes, yellow stars, or baffles spaced at a regular interval) to find a feeder. Irrespective of the shape and color of the landmarks, honeybees searched for food at the correct position, between the third and fourth landmarks [55].

Using an appetitive-aversive conditioning paradigm (i.e., correct stimulus associated with positive reward and incorrect stimulus associated with punishment), honeybees were able to correctly perform simple arithmetic operations in a delayed match-to-sample task (i.e., add/subtract one element from a numerical

Fig. 1. Evidence of the presence of a *sense of number* has been documented in various invertebrate species: (1) mealworm beetle (*Tenebrio molitor*) prefer the substrate bearing the odors of the larger number of females. (2) Ladybirds (*Coccinellidae*) choose the best laying spot according to the number of conspecific larvae and quantity of food (i.e., aphids) available (3) When they have lost the higher number of prey, spiders (*Nephila clavipes*) spend a higher amount of time searching for their food. (4) Bumblebees (*Bombus terrestris*) can discriminate between visual sets using numerical information, and transfer their learning to novel stimuli differing in shape and color. (5) Cuttlefish (*Sepia pharaonis*) prefer the larger number of shrimps when presented with dual-choice tasks, even when the numerical comparison involves fractions (e.g., 1 *vs.*1.5 shrimps). (6) Solitary bees (*Eucera*) seem to use also numerical information to adjust their foraging departure strategy, avoiding returns to nectaries already visited. (7) When an ant (*Formica polyctena*) returns to the nest, its antennal contact with the nestmates lasts longer if the ant has passed a high number of branches on the way back. (8) Honeybees (*Apis mellifera*) use numerical information during navigation, process the zero quantity, perform simple arithmetic operations, and transfer a particular learning across dimensions (i.e., from number to space). All the images shown in this figure are from public domain (Wikimedia Commons). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

sample). Bees were presented in a Y-maze with a colored sample number. If the sample was blue (i.e., showing either 1, 2, or 4 blue elements), bees had to choose the one-element larger array in the subsequent numerical comparison in order to be rewarded (i.e., to choose 2, 3 or 5 blue elements as correct). Conversely, if the sample was yellow (i.e., showing either 2, 4 or 5 elements), the bees had to choose the one-element smaller array in the subsequent comparison (i.e., choose 1, 3 or 4 yellow elements as correct). At test, bees were presented with a novel sample number (i.e., 3) whose color determined the correct choice of the smaller (yellow) or larger number (blue) in the next comparison. Bees were able to successfully transfer the arithmetic rule (blue = add, yellow = subtract) to novel numbers, suggesting an ability to use symbolic cues to solve basic arithmetic operations with small numbers (up to 5 units) [69].

Another important building block of numerical cognition is the ability to understand the concept of zero as a numerosity (i.e. as an “empty” set). Until recently, this ability was thought to be a prerogative of primates such as rhesus monkeys [68–71], vervet monkeys [72], chimpanzees [73] or of bird species such as the African grey parrot [74]. Honeybees and ants also showed the capacity to process a non-symbolic concept of zero numerosity by correctly placing a blank stimulus at the beginning of the numerical continuum [75,76]. Bees were divided into two groups and trained to choose either the smaller or the larger of two numerosities (i.e., from 1 to 4 units) across trials. At test, they were presented with a novel comparison between an empty set (i.e., containing no elements) and a novel array containing some items (i.e., from 1 to 4 items). Honeybees previously trained to apply the “smaller than” rule, consistently chose the empty set, considered as lower than the other numerosity, while the “larger than” group chose the novel set containing the other elements. Bees trained to choose the *less than* numerical value, preferred the empty set even when compared with the one element. Besides, the zero appeared as placed along a positive numerical continuum because the discrimination accuracy of bees was higher for 0 *vs.* 5 and 0 *vs.* 6 discriminations and lower for 0 *vs.* 1 or 0 *vs.* 2 discriminations, showing the typical *numerical distance* effect [75].

Bees are not the only insects showing numerical abilities [77]. Desert ants (*Cataglyphis fortis*) can use numerical information to keep track of the distance covered during navigation activity. Wittlinger and collaborators (2006) hypothesized the existence of a “step counter” that allows the measurement of the distance intercourse from the nest to a food site. To test this hypothesis, the leg’s length of the ants was manipulated by either increasing or decreasing it (i.e., adding stilts or creating stumps), resulting in longer or shorter steps made by walking ants. When released from the food site, ants with longer legs searched for the nest after having walked a longer distance, while shortened-leg ants searched for the nest at a shorter distance, thus suggesting the use of a “step counter” to calculate the itinerary distance [54]. Scout ants (*Formica polyctena*) seem to communicate the numerical information in order to find food placed in a series of identical sites. Forager ants were randomly placed in one of 25–60 equally spaced branches where they could feed. The ants would then return to the nest and make antennal contact with the nestmates. Such contact lasted longer according to the number of branches the ants had passed on the way back to the nest [78].

Insects are not the only artropods being able to use numbers. Spiders (*Portia africana*) change their predation strategy according to the number of conspecifics at a prey’s nest, preferring to settle when the number is one instead of zero, two or three in order to maximize their probability of hunting success [58]. The relationship between numerical cues and searching behavior of another species of spiders (*Nephila clavipes*) was also investigated. These spiders were given the possibility to choose between 1, 2 or 4 small preys, or one single large prey. The total area was equated between groups with different numerosity, in order to minimize the influence of confounding variables. Later, the preys were removed and the searching time of spiders was recorded. The results showed that spiders spent more time searching for food when they had lost the greater number of prey, highlighting the importance of computing numerosity in their food choice [59].

3. Insight from an insect’s brain: transfer from number to space

The hypothesis of a general framework that allows the processing of number, space and time has not yet been fully tested in invertebrates. However, some recent evidence on honeybees seems to suggest the presence of a transfer between discrete and continuous dimensions in an insect species, laying the groundwork for further research.

Honeybees are the ideal invertebrate model to investigate the existence of a general magnitude mechanism because their ability to process separately different magnitudes as number, space, and time has already been attested. Apart from their well-established numerical abilities, described above (and see also [3]), bees have the ability to discriminate stimuli with different size by choosing the larger or the smaller stimulus in comparison tests [79,80]. They can discriminate between sources that provide food at a different time of the day [81] and they discriminate between moving and stationary stimuli [82] and between specific flashing temporal frequencies (i.e., showing preference for 20–25 Hz frequencies and avoidance of 50–100 Hz and 2–4 Hz frequencies; [83]).

In an attempt to document the universality of a coding for magnitude, Bortot and collaborators (2020) trained free-flying honeybee foragers to associate a reward with either the larger or the smaller numerosity in various numerical comparisons (2 *vs.* 4, 2 *vs.* 3, 4 *vs.* 8, and 4 *vs.* 6) with a different ratio (i.e., 0.5 or 0.67). At test, bees were then presented with a choice between visual stimuli displaying the same number of objects but of different sizes (e.g., bees trained to select 4 over 8 elements, were presented with a 4 *vs.* 4 comparison where one group of elements was twice the size of the other group). The results suggested that irrespective of the ratio of the comparison, bees trained to select the smaller or the larger numerical quantity chose the smaller or larger size respectively, thus documenting for the first time the presence of a cross-dimensional transfer from a discrete (i.e., number) to a continuous (i.e., space) dimension in an invertebrate species [84]. This study leads to further questions, as to whether the transfer can be observed also the other way around, i.e. from number to space, or using other magnitudes, and whether a similar transfer could be found in other invertebrate species.

4. Conclusion

The study of invertebrates opened questions as to whether they possess cognitive abilities similar to those observed in vertebrates. The presence of cognitive capacities in invertebrates that rival those of vertebrates, does not exclude the possibility that the two taxonomic groups might rely on the use of different strategies. Careful control of all possible confounding factors, as well as thoughtful planning of the experimental design, appear necessary (see the debate between [85,86]).

Animals with miniature brains like invertebrates can perform a wide range of complex behaviors. Honeybees, for example, can deal with same/different [87] and above/below concepts [88]. These findings promoted research on artificial neural networks inspired by the simple structure of the invertebrate neural systems to the aim of modelling and better understanding the neural basis of cognition. Cope and collaborators (2018), for instance, developed an artificial network constrained by the relatively well-known neural properties of the mushroom bodies of honeybees. The network appeared to be able to learn abstract concepts, such as sameness and difference, with learning and performance rate similar to those of real bees [89]. Neural network studies can be used for investigating the foundations of numerical abilities as well. An insect-inspired artificial network with only four neural units can process numerosity information, reproducing the behavioral findings obtained in bees trained to a *smaller than*/*larger than* rule task and then tested for their ability to encode the zero numerosity in the numerical continuum [88,90]. Similar to bees [75], the network was able to form concepts such as “larger”, “smaller” and “zero” when associated with a sequential flying scanning behavior, a strategy used by bees to inspect visual items [49,67]. Moreover, the network accuracy in discriminating two numerical stimuli increased as the numerical distance between the items increased, thus reproducing the *numerical distance* effect [90].

A recent study explored the possibility to discriminate quantities in a single spiking neuron model. The results showed that a single neuron solves numerical tasks (i.e., accurate counting of the number of items in two visual arrays and application of the *greater than* rule to select the larger quantity) exhibited by insects such as bees, by relating the number of elements in the array with the sum of its spikes. The representation of numerical cues through neural spikes could be an adaptive strategy implemented in invertebrates to spare on the number of neurons recruited in complex tasks [91].

With their peculiar behavior and lifestyle, invertebrates are considered amongst the most remote organisms from humans. This gap makes it harder to approach and understand these creatures' mind, ultimately underestimating their capacities [48]. However, the study of invertebrate cognition has highlighted the presence of numerical abilities once believed a unique prerogative of humans and other vertebrates. Furthermore, invertebrates proved a valid model for the investigation of the evolutionary pathway and of the ultimate function of numerical cognition, and for the development of artificial intelligence systems mimicking their smaller, but no less complex, brain structure. A forthcoming research goal would be clarifying the mechanisms supporting numerical abilities in invertebrates, to understand whether a general and unitary mechanism to deal with magnitudes is also present in these smaller-brained species.

Declaration of competing interest

The authors of the manuscript declare with the present statement that there is no conflict of interest concerning all information reported in the manuscript.

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