Ecological decision-making: From circuit elements to emerging principles

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Abstract
The interactions an animal has with its prey, predators, neighbors, and competitors are known as ecological interactions. Making effective decisions during ecological interactions poses fundamental challenges for the nervous system. Among these are the need to filter relevant information out of complex and ever-changing sensory scenes, to balance competing objectives, and to generate robust behavior amid the strong mutual feedbacks that occur during interactions with other animals. Here, I review recent advancements in the study of ecological decision-making. Using research with fishes, I illustrate how knowledge of ethology and brain circuitry are converging to yield a more holistic understanding of how the brain solves these problems to produce robust sequences of natural behavior.

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Introduction

As we move through the world, we change our behavior based on the sensory stimuli we experience, the physiological states we enter and exit (e.g., hunger, stress), our encounters with other people, and an ever-evolving set of short and longer-term goals. Likewise, following an animal around its natural habitat reveals rich patterns of behavior that include fast and slow transitions among activities, apparent shifts in priorities, and, importantly, diverse interactions with other animals (Figure 1). The dynamic sequences of behavior we and other animals produce over the course of a day require thousands of decisions. Determining how these decisions are made—both in terms of the behavioral algorithms by which sensory information leads to one behavioral action or another, and in terms of the properties of neural circuits that control these actions—is at the heart of what it means to understand how the brain generates behavior [1].

The past few years have seen a renaissance of interest in ecological decision-making, the process by which animals make decisions during natural interactions with prey, predators, neighbors, and competitors. This trend is due, at least in part, to two recent innovations: qualitative leaps in the precision with which the actions of unrestrained animals can be measured [2], and new methods for making in vivo measurements of the nervous system during naturalistic behavior [3—8]. Here, I review recent advancements in our understanding of ecological decision-making. I focus on studies of fishes, which have served as a model system for researchers seeking to connect neural circuits with sequences of ecologically meaningful behavior.

Parsing sensory scenes and the cocktail party problem

In nature, animals make decisions across an unthinkably broad range of sensory conditions. Across all this variability, an animal must retain the ability to learn about relevant events in the environment such as the approach of a predator or the actions of nearby conspecifics. Doing so involves identifying and isolating the stream of sensory data relevant to an event of interest from a complex, dynamic background. This task has been referred to as "the cocktail party problem" [9], in reference to the challenge of focusing on an individual speaker amid the din of a crowded cocktail party. The cocktail party problem is integral to ecological decision-making; without isolating and spatially localizing sensory input from a given source, processes like feedback control for pursuing prey [6,10,11] or goal-directed escape responses [12] would be impossible. Through work in fishes, particularly in the visual system, a picture of how the brain solves this problem is coming into view (Box 1).

Figure 1
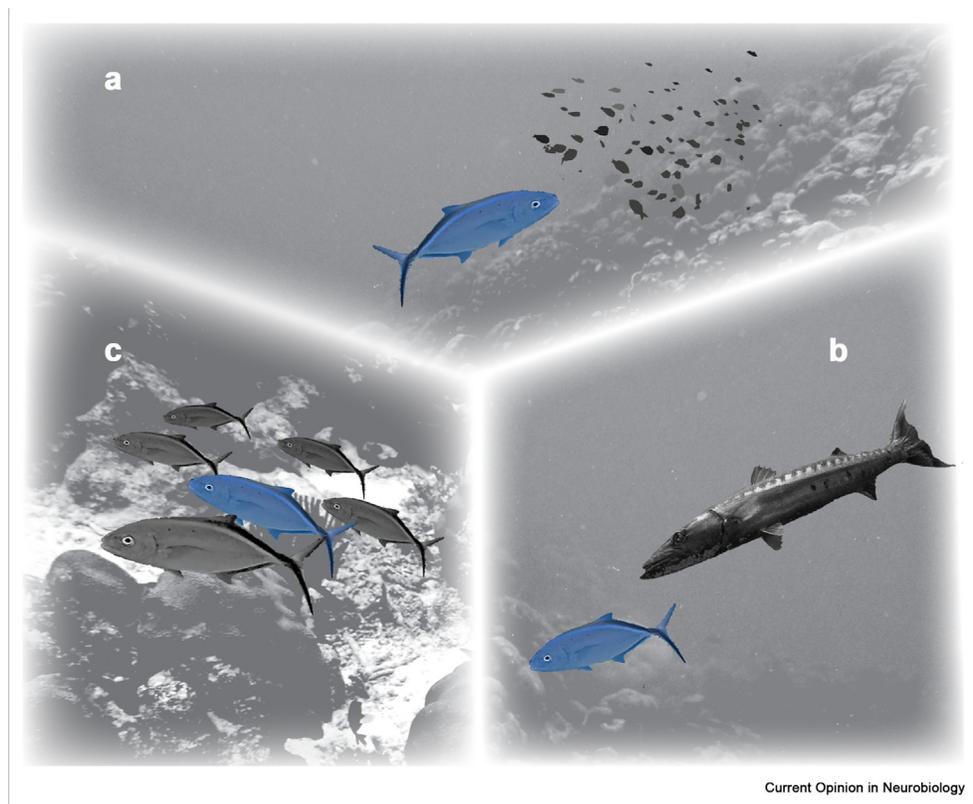
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Shifting priorities and sensory demands during ecological decision-making: (**a**) hunting behavior (**b**) predator evasion and (**c**) social interactions.

The fish visual system filters sensory scenes through a highly parallelized processing scheme that adjusts to changing statistics of a visual scene on timescales ranging from tens of milliseconds [13] to many minutes [10,14]. The structure of this system reveals two properties likely to be important for ecological decision-making. First, raw stimulus measurements are reconfigured into *sensory features* early in sensory processing, often within or near the sensory organ itself (Box 1 [13,15,16]). Sensory features include things like the size, motion, and patterning of visual objects. Importantly, the dimensionality of feature space is far lower than that of raw visual input space. Computations to determine which features are relevant and which are not begin almost immediately, through the action of distributed microcircuits that make comparisons between sensory features over time and across visual space [13,15]. The second key property is that sensory features associated with different types of event in the environment are simultaneously processed through distinct pathways in the brain [8]. For example, stimuli associated with prey and stimuli associated with predators are encoded by distinct sets of retinal ganglion cells, and processed through distinct, spatially segregated pathways in the tectum (Box 1 [16]). Processing

within these parallel pathways, and competition between them ultimately determine how the animal will respond [4,15,17,18].

Ecological decisions must be made quickly [11], but they must also be robust to complex, dynamic, and often novel sensory scenes. The properties of the fish visual system suggest a strategy by which the brain overcomes these challenges. By computing visual features through distributed circuits in the retina and tectum, information relevant to different types of behavioral actions (e.g. approach or avoid) are extracted simultaneously in a way that maintains sensitivity to novel stimuli as the scene changes [19,13]. By processing these features through distinct pathways, evidence for different types of ecological events can be accrued rapidly in parallel, compared across pathways, and used to select an action [18].

Balancing competing objectives: From action-selection to changing brain states

Tradeoffs are another ubiquitous feature of ecological decision-making. Tradeoffs in ecological tasks are rarely simple. They often require an animal choose between engaging in very different types of activities, with costs and rewards that are experienced over

Box 1. Processing and filtration in the fish visual system.

The fish visual system has become a model for understanding how the nervous system filters and processes sensory scenes. The first layer of filtration occurs through the spatial organization of sensory receptors. In the fish eye, photoreceptors with distinct spectral sensitivities are heterogeneously distributed across the retina in ways that are matched to the typical spectral properties of incoming light in different regions of the visual field ([52], Box Fig.). Rather than being transmitted to the brain in raw form, the information captured by receptors is immediately reorganized into sensory features, for example, the size, motion speed and direction, and local contrast polarity of a visual object [17,53]. Cells in the retina also encode larger-scale features such as spatial patterns and changes in such patterns [13].

After sensory features are computed, they are transmitted by retinal ganglion cells (RGCs) in parallel to the brain in a fashion that preserves the spatial locations of features [54,55], but segregates features associated with events that require different kinds of responses into distinct pathways [8,16−18,53,54] where features are further processed and recombined [53]. In the fish tectum (also known as the superior colliculus), a central relay and processing station for incoming sensory data in the fish midbrain [56], small size and motion-selective RGCs terminate in superficial tectal layers [16], whereas features associated with expanding objects terminate in deeper tectal layers [57,16]. Downstream neurons in the tectum integrate feature-selective inputs from multiple RGC types, and in some cases, sharpen specificity for certain object features (e.g. specificity to small moving objects [16]). Additional modification of tectal processing is provided by other brain regions including the thalamus [5] and hypothalamus [4]. Another stage of filtration occurs in premotor regions in the hindbrain, where recurrent [4] and lateral inhibitory circuit motifs (e.g., between Mauthner cells [58]) exert additional control over whether a given stimulus will lead to motor behaviors, and what type of motor response will be executed [59]. Finally, whether an animal responds to a given sequence of stimuli depends on modulation of decision-making circuits on longer timescales, often across multiple brain regions [14,7].
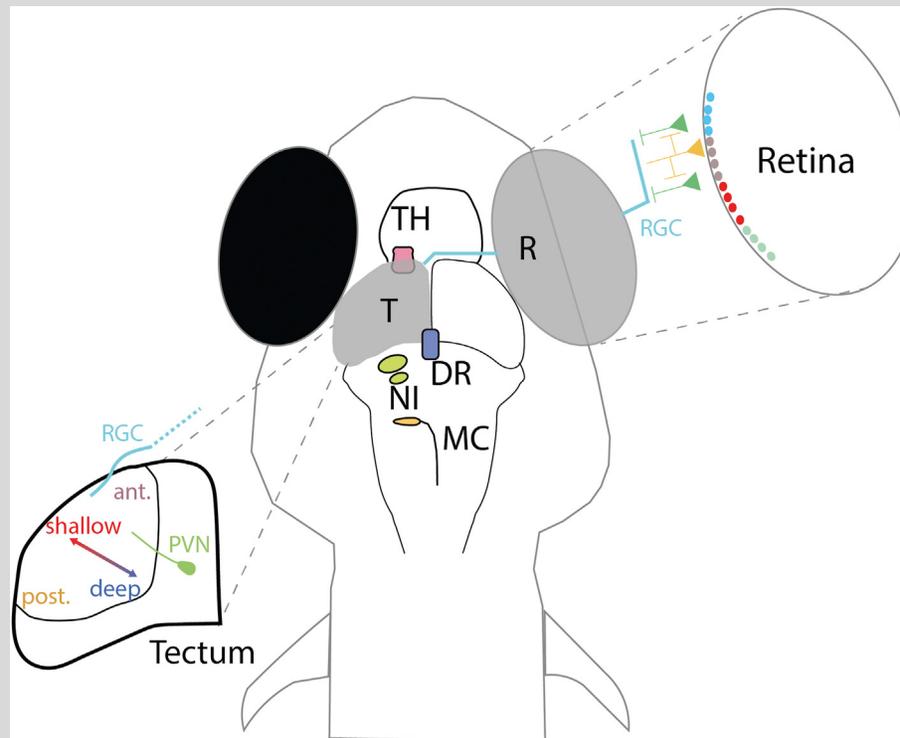
Elements of the fish visual system showing selected structures and brain regions: eye with retina (R), retinal ganglion cell (RGC), tectum (T), thalamus (TH), nucleus isthmi (NI), dorsal raphe (DR), and mauthner cell (MC). Optic nerve from right eye projects to the left tectum and only brain regions corresponding to that visual hemisphere are shown. Retina inset shows heterogeneous distribution of photoreceptor types across the retina [52] and retinal portion of retinotectal microcircuits, which compute visual features [13] and salience among visual objects [15]. Tectum inset shows RGC projecting to the tectum. Anterior−posterior and shallow−deep axis of tectal neuropil, and preventricular neuron (PVN) are also shown. Anatomy reproduced from the studies by Marques et al., Forster et al., Henriques et al., Isa et al., Shimazaki et al. [7,16,23,56,58].

different time horizons [1]. Selecting the best of a set of alternative actions when feedback is delayed [20], or when different options produce feedback on different timescales is a notoriously challenging problem in machine learning. The fact that animals routinely make such choices during ecological interactions has led to significant interest in this facet of ecological decision-making.

Explore or exploit

Whether to exploit a known option or to explore other, less familiar options is a common tradeoff faced during decision-making [21]. Marques et al. [7] studied this tradeoff using whole-brain imaging of freely-swimming zebrafish in arenas containing *Paramecium* prey. They found that larvae transition between two behavioral states, termed "exploration" and "exploitation," during which movement and hunting behaviors differ markedly, and brain-wide patterns of neural activity are distinct. The exploitation state is strongly correlated with activity of a population of neurons in the dorsal raphe nucleus (Box 1 Fig.), and transitions between states are correlated with activity of a trigger network also involving the dorsal raphe, which can become active spontaneously or in response to events such as changing light levels or successful prey capture [7].

Another manifestation of the exploration—exploitation tradeoffs occurs within natural hunting sequence themselves. When hunting prey, predators abort a large fraction of pursuits without even attempting to strike prey [22,23,10]. In zebrafish, the onset of hunting bouts coincides with elevated activity of neurons in the nucleus isthmi (NI, Box 1 Fig.), a nucleus that reciprocally connects to regions of the optic tectum involved in visual processing during hunting [23]. The properties of NI connections to the tectum are consistent with the hypothesis that the NI controls sustained hunting behavior by enhancing visually-evoked neural activity in tectal pathways, possibly by enhancing transmission of visual stimuli from RGCs to the optic tectum. One possible function of this is to tune hunting behavior based on an animal's hunger level. For example, hunger-induced recruitment of tectal neurons that respond to prey-sized moving objects [24] could increase input from the tectum to the NI when an animal is hungry [10]. NI feedback to the optic tectum could then cause hungry animals to extend hunting bouts, as observed in starvation experiments [10].

Feed or flee

In nature, deciding when to continue feeding and when to flee is a matter of life or death. At the most basic level, balancing this tradeoff requires that an animal distinguish food from threats [18], a task that is not always as trivial as it might seem [25]. Larval zebrafish exhibit distinct approach and avoidance behaviors to moving visual objects, and whether the response is positive (approach) or negative (avoid) depends on the object's size [18,24]. Interestingly, the relationship between object size and behavioral response changes markedly when an animal is hungry. Starved fish approach small objects more frequently and are less likely to avoid objects of intermediate size [24]. This hunger-driven shift in behavioral valence is controlled, in part, by

hypothalamic—pituitary—adrenal activity, which modulates size response properties of visually-activated neurons in the optic tectum. In hungry animals, reduced cortisol and enhanced serotenergic transmission promotes recruitment of additional tectal neurons sensitive to small object sizes [24]. This increased activity of tectal neurons may act both by heightening sensitivity to stimuli prey-associated stimuli and by inhibiting a competing pathway involved in avoidance behavior [18].

Perception of risk

The costs and benefits of making a particular decision depend not only on an animal's internal state but also on the external environment. Changes in decision-making in "risky" versus "safe" environments are widely documented [26]. But if an animal is to modify its behavior based on risk, it needs a way to measure risk. One such measure is the presence of other nearby individuals. Wild coral reef fish feed for shorter periods of time between retreats to shelter when foraging alone than when they forage in large groups [27]. When these animals are exposed to acute threats (looming visual stimuli), responses depend on visual stimuli from the threat *and* visual stimuli produced by neighboring individuals [12]. This implies a mechanism for tuning escape decisions on a fast timescale based on perception of neighboring individuals. How might such context-dependent responses be controlled in the brain? One possibility is that when nearby individuals and other stimuli are viewed at the same time, competition for salience reduces the overall likelihood of responding to any of the stimuli. This could occur, for example, through reciprocal inhibition between competing stimuli within the retina [15].

On slower timescales, isolation from conspecifics causes oxytocinergic activity in the hypothalamus [28]. This activity appears to increase activation of premotor neurons in the hindbrain including Mauthner cells (Box 1 Fig.) and other reticulospinal neurons that control motor behavior [29]. Oxytocinergic activity is associated with an increase in defensive behaviors and a decrease in feeding, suggesting that social isolation may promote behaviors such as escape responses, but that it also simultaneously suppresses appetite.

To make effective decisions, animals must balance tradeoffs. Doing so requires that the animal account for its current needs as well as how its actions will influence the likelihood of different outcomes. The latter is determined at least partly by the state of the environment. A widespread finding is that internal state controls action-selection not simply by favoring one action or another in the final stages of decision-making, but also by changing how incoming sensory data are processed [24]. Similar processes may govern changes in decision-making as the state of the environment

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Box 2. Hunting and feedback control

Hunting prey is a an ecological task that requires an animal make a sequence of decisions—detect prey, initiate pursuit, control pursuit movements, and execute a final strike—to receive a reward. Like larvae of other fish species [47], larval zebrafish hunt live zooplankton, and this behavior has become a model for understanding behavioral control [53,6,48,49].

Zebrafish hunting bouts follow a characteristic progression. Larvae typically first respond to prey viewed in the frontal visual field [6,49,46]. Following prey detection, larvae exhibit characteristic "j-turns" that move the prey toward the proximal, dorsal region of the visual field. This phase of hunting also involves convergence of the eyes [53], a behavior that increases the zone of binocular overlap in the proximal region of the visual field. Hunting sequences end with either an abort [23] or with a terminal attack maneuver [6,10,46]. Larvae typically launch terminal attacks when prey are within 0.4−0.6 mm of the head, near an azimuthal angle of zero, and located slightly above them in the water column [6,46], and larvae will dive if necessary to position prey in this zone [46]. Importantly, hunting behavior requires visual feedback, and the removal or temporal disruption of this feedback in virtual prey experiments results in aborted [6] or disrupted [60] hunting sequences.

Larval fish face a challenging control problem when hunting fast-moving prey [47,6], but strong mutual feedbacks between predator and prey are even more pronounced during hunting behavior of adult fish. When hunting evasive prey, predatory bluefish (*Pomatomus saltatrix*) continuously adjust swimming trajectories as prey move, presumably using visual feedback [61]. Interception trajectories of bluefish are consistent with a strategy known as "deviated pursuit" in which the pursuer turns continuously to align its velocity vector with the line-of-sight to the prey plus a small offset angle. These predators also accelerate to high speeds during the terminal phases of attacks, possibly in response to evasive maneuvers of prey.

Among the primary challenges bluefish and other predators face when pursuing evasive prey is that posed by sensory-motor delays: the delay between perception of sensory stimuli and motor responses to those stimuli [62]. Because of such delays, a predator's movement at any given time is based on past observations of prey. Computational models of predator−prey pursuit−evasion interactions suggest that sensory-motor delays are among the most important constraints limiting the success of predator attacks [11]. One way for a predator to cope with delays is to steer based on a prediction of future prey locations rather than using only currently perceived prey location. Bolton et al. [46] found evidence of such prediction in the hunting maneuvers of larval zebrafish, which modulate their steering and acceleration based not only on the locations of moving prey but also on perceived prey motion. Forecasting the position of a moving object require that an animal combine position and velocity information. Although the fish visual system encodes variables related to these quantities [53], the neural mechanisms through which these variables are combined to produce a forecast remain unclear.

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changes [29,28]. An important future step will be determining whether these mechanisms for tuning responses are simply crude heuristics, or whether they are based on encodings of the key quantities required to optimally balance tradeoffs: the quantitative values of different outcomes [30], and the probabilities of those outcomes given one action or another [21].

Decision-making and mutual feedbacks

Another characteristic of ecological decision-making is that it often involves strong mutual feedbacks between interacting animals. We have all experienced such feedbacks when trying to avoid colliding with someone walking in the opposite direction on a sidewalk. You veer left and so does your counterpart. You correct right, and so does she. In the presence of a telephone pole or a mailbox, this problem does not arise. Such mutual feedbacks occur during many ecological behaviors including competition for food, hunting mobile prey (Box 2), and, in an extreme form, during social behaviors such as schooling [31] and feeding aggregations [27].

Schooling, aggregations, and feedbacks

Grouping with others has well-documented benefits such as diluting the risk of predation [32], but neighboring individuals also produce large quantities of sensory stimulation [33,34]. Sensory cues from neighbors can be beneficial [31,32], but they also create the potential for the actions of an animal to feed back on it through the responses of its neighbors, a process that can be thought of as form of reafferrence.

Schooling golden shiners (*Notemigonus crysoleucas*) make movement decisions based on the spatial locations of nearby individuals using rules that are consistent with continuous feedback control [35,36]. By adjusting acceleration, deceleration, and turning based on neighbor locations, animals maintain fairly consistent positions relative to neighbors [35,37], potentially minimizing the risk of creating strong stimuli that could feed back by producing large changes in neighbor behavior (but see the study by Tunstrøm et al. [38]). More recent work suggests that the behavioral algorithms that guide movement decisions in schools can be produced by relatively simple responses to visual stimuli from neighbors [39,40,34], that these algorithms change predictably over ontogeny [41,40,34], and that they appear to be heritable [40]. A heuristic model of the core computations involved in visual schooling behavior was recently proposed [42]. However, the details of how these computations may be carried out in the brain are not yet clear. Interestingly, mutations known to impact other aspects of social behavior also affect how fish

transform stimuli from neighbors into movement decisions [40]. These disrupted movement rules alter collective behavior of groups of individuals.

In contrast to the behaviors fish employ during routine swimming, the behavioral algorithms used during behaviors such as collective escape responses can produce strong bursts of sensory stimulation perceptible by neighbors [39,43]. During collective escapes, one or several individuals in a group typically accelerate [44] creating stimuli that can cause cascades of startle behavior [44,39,43]. Notably, the influence of neighbors on any given focal individual are often highly unequal [39,43], suggesting that some mechanism for selectively attending to a dominant neighbor [15,45] or unequally weighting neighbor stimuli [42] may be important for controlling responses.

Many ecological behaviors involve mutual feedbacks (Box 2). In comparison to other aspects of decision-making, we know relatively little about how animals control behavior amid such feedbacks. Selective attention [15,45], behavioral averaging [42], and forecasting future positions of moving targets ([46], Box 2) are candidate mechanisms that could help animals retain behavioral control in these situations. But our understanding of how these mechanisms are implemented in the brain and integrated to produce behavior are far from complete.

Conclusions and outlook

The current resurgence of interest in ecological behavior is exciting, to be sure. But where will future work on the ethological, computational, and neural aspects of ecological decision-making lead us? Put another way, by studying ecological decision-making, what is it, exactly, that we wish to understand?

One answer is that the ability to produce sequences of effective decisions across a vast range of novel conditions is among the most conspicuous, yet least understood aspects of natural behavior [1]. By studying ecological decision-making, we seek principles of brain function that make this simultaneous flexibility, robustness, and generalizeablity possible. Larval fish produce hunting sequences to capture mobile prey within days of hatching [47,48] even on the first exposure to live prey [49]—a feat tantamount to few-shot or even zero-shot learning. Likewise, fish respond to novel threat stimuli by generating escape behaviors that balance competing objectives [15] and shift seamlessly from one proximate task to another [12] in ways that appear to sidestep challenges such as constraint violation and catastrophic forgetting that plague artificial decision-making systems [50,51]. Here, I have argued that three general properties of neural circuits help explain how decision-making in these tasks can be fast, robust, and flexible all at the same time: distributed computation of sensory features [13,15], parallel processing of sets of features by distinct, often competing pathways [8,16,18], and slower-timescale modulation of decision-making circuits based on internal and external states [7,24,28]. Are these circuit properties so fundamental that we should consider them principles of brain organization that enable effective natural behavior? Further comparative work, as well as targeted computational studies of these properties could go a long way toward answering this question.

Recent progress notwithstanding, there remains so much to learn about how animals make ecological decisions. We need principles to help organize the central challenges involved in ecological tasks, and the mechanisms by which nervous systems overcome these challenges. This is particularly true for decisions that involve interactions with other organisms that are, themselves, sensing and responding. In nature, interacting brains are the rule rather than the exception [31,32]. The strategies the nervous system has evolved to guide decision-making must, therefore, account in some way for the decisions of other agents with both aligned and conflicting interests. While related questions have been addressed through work in social psychology, evolutionary game theory, and collective behavior, we still lack an understanding of the computational principles that allow the brain to produce dynamic sequences of decisions amid strong mutual feedbacks. Future studies are poised to change this, opening up a suite of new and exciting questions whose answers will teach us much about behavior and brain function alike.

Conflict of interest statement

The author declares no conflict of interests.

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