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The cognitive basis of individual recognition

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Individual recognition allows animals to discriminate among individuals and adjust their behavior accordingly. It involves the production and propagation of individually-distinctive signals or cues and then the perception and recognition of those signals or cues. This review highlights recent work investigating this process, emphasizing the cognitive basis of perception and recognition. It finds that relatively few studies have addressed how signatures propagate through the environment and are processed by the receiver. Given variation across species in the complexity of recognition, this review recommends further comparative studies be conducted to unravel the factors underlying this variation.

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Introduction

Recognition is important for social animals so that they can discriminate among individuals and categorize them as offspring, mates, rivals, group members, social partners or neighbors [1–3,4•,5•]. It involves a sender producing a cue or signal and a receiver perceiving that cue or signal; the receiver then identifies the sender based on the perceived information and exhibits a behavioral response (Figure 1; [6,7]). Recognition varies along a continuum such that animals can recognize groups of individuals (class-level recognition) or specific individuals (individually specific recognition; [3,4•,5•]). Individually specific recognition includes recognition of a single individual (such as offspring when there is only a single offspring or a mate when there is only a single mate) or multiple individuals (such as each individual within a social group; [7]). The aim of this article is to review recent work investigating individually specific recognition (hereafter 'individual recognition'), focusing on the production, propagation, perception, and recognition of individually-distinctive signals or cues ('signatures'; Figure 1). While many studies have examined signature production, fewer have addressed how signatures propagate through the environment and are processed by the receiver. This review highlights areas where additional research would enhance our understanding of individual recognition.

Production of signatures

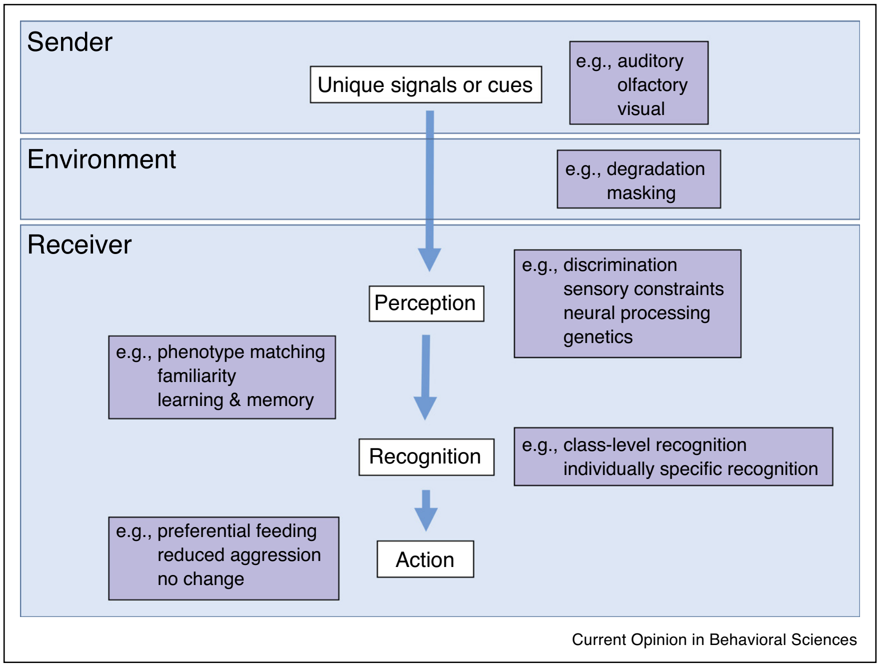
Consistent variation in signatures both within and across individuals is a prerequisite for individual recognition [1]. Many studies have demonstrated that individuals across different taxonomic groups produce signatures [4•]. Within the past several years alone, signatures have been demonstrated in apes [8], bats [9,10], birds [11–16], deer [17], elephants [18], frogs [19], mice [20], monkeys [21–23], penguins [24], rhinoceros [25], and whales [26]. These signatures are emitted in a wide range of contexts [27], including parent–offspring interaction [9,12,17], group cohesion [10,15,25], courtship [11], predator defense [22], and territory defense [20,21,23].

Signatures are emitted in different modalities and therefore differ in their signaling properties [27]. Acoustic signatures can function in long-distance communication. For example, the loud calls of howler monkeys (*Alouatta pigra*) contain individually-distinct acoustic properties and can travel long distances [23]. Chemical signatures conveying identity information can persist in the environment for extended periods. As an example, male mice (*Mus musculus*) deposit urine in the environment that is individually unique; other males can detect this chemical signal even after the original male has left the area [20]. And, visual signatures are effective in close-range interactions. Large-billed crows (*Corvus macrorhynchos*), for example, have individually-unique facial configurations that they can potentially use to discriminate each other [14]. Based on this extensive work examining signature production, it is firmly established that individuals across different species produce signatures and our research focus should shift to examining the environmental effects on signatures and their perception and recognition by receivers.

Environmental effects

The environment through which signatures are propagating can influence identity information. Acoustic signatures are especially susceptible to environmental degradation [28,29]. For example, zebra finches (*Taeniopygia guttata*) use loud calls to communicate with their mates [28]. At long distances, however, some acoustic properties of the calls are significantly degraded as they propagate

Figure 1



The cognitive process underlying individual recognition. Senders emit signatures, which propagate through the environment, that receivers can use to extract information about the specific identity of the senders.

through the environment and this may impair mate recognition. Despite environmental degradation, zebra finches can learn to recognize acoustic signatures. Female zebra finches become more accurate in recognizing their mate's degraded calls when they have exposure to those calls [29]. Anthropogenic noise pollution may also negatively impact the ability of animals to recognize each other by masking signatures [30]. There is a lack of research examining the impact of environmental factors on individual recognition in other modalities. However, it is likely that visual and chemical signatures are also impacted by environmental conditions. Reduced lighting levels and temperature changes could impair animals' ability to visually and chemically recognize each other, respectively [31,32]. Additional studies examining environmental effects, both natural and anthropogenic, on individual recognition are needed.

Perception of signatures

If animals produce signatures that effectively propagate through the environment, receivers that perceive these signatures can potentially recognize individuals. Many studies have demonstrated that animals can discriminate among signatures emitted by different individuals. For example, based on a habituation–discrimination paradigm, apostle birds (*Struthidea cinerea*) and peahens (*Pavo cristatus*) can discriminate among individual callers [33,34] and domestic horses (*Equus caballus*) can discriminate among individual scents [35]. And, using a training paradigm, European starlings (*Sturnus vulgaris*) can discriminate between the calls of a specific individual among other conspecifics [36].

By modifying the properties of signatures, we can begin to understand the exact features that animals are discriminating among [37,38]. This is important because, even if a signature component is individually unique, receivers may not use that component or they may be unable to use it in discriminating among individuals due to sensory constraints. For example, individual differences in an acoustic parameter may exist but cannot provide identity information if receivers are not sensitive to it [39] and therefore unable to detect the differences.

The neural and genetic processes underlying the perception of signatures are unknown in most species despite their importance to our understanding of how animals recognize each other. However, one study uncovered a neural region in birds associated with recognizing individuals [40]. European starlings trained to recognize the songs of a specific individual are impaired in their ability to do so when they have lesions to their HVC. While studies investigating the genetic basis of individual recognition have not been conducted, researchers have begun examining genetic factors contributing to class-level recognition [41,42]. Berens *et al.* [14] identified candidate genes related to calcium signaling that are involved in discriminating between familiar and unfamiliar wasps (*Polistes fuscatus*). Because of recent advances in neurobiology and genetics, further research investigating the neural and genetic mechanisms of individual recognition should be possible.

Recognition

Animals that perceive differences among individuals based on signatures can rely on familiarity to recognize them [27]. Animals can recognize individuals through familiarity by interacting with them and habituating to or learning their specific traits [5•]. This mechanism of individual recognition is considered cognitively demanding, especially to the receiver [43,44]. Learning and memorizing features associated with individuals likely expends energy and nutrients, occupies times, and increases predation risk [45]. The mechanisms underlying individual recognition and the cognitive costs associated with them remain unexplored in many species and therefore offer a promising area for additional investigation.

Few studies have investigated whether animals use information contained in signatures to recognize individuals. Playback experiments are one method that can be used to test for individual recognition. For example, fur seal pups (*Arctocephalus tropicalis*) quickly learn to recognize their mother. The pups vocalize more in response to their mother's calls compared to strangers' calls [46]. As another example, spectacled parrotlets (*Forpus conspicillatus*) recognize their mate. They emit more contact calls upon hearing the call of their mate compared to the calls of other conspecifics [47]. While this playback method is useful for demonstrating individual recognition when receivers are only recognizing a single individual, it is not ideal for investigating individual recognition when receivers are recognizing many different individuals.

One of the most promising methods for testing individual recognition of many different individuals involves using a cross-modal approach (Table 1). Animals are exposed to a signature from an individual in one modality; they are then exposed to another signal or cue from either the same individual ('congruent') or a different individual ('incongruent') in another modality. Animals that demonstrate individual recognition react differently to the signatures when they are incongruent compared to congruent [51]. In a recent study, Gilfillan *et al.* [48] found that African lions (*Panthera leo*) demonstrate cross-modal individual recognition. Lions reacted strongest to an incongruent situation in which roars from an individual lion did not match with the lion that was previously seen at that location. Cross-modal recognition has even been shown between distantly-related species [49•,52,57]. Proops and McComb [52] showed that domestic horses (*Equus caballus*) spent more time looking at a familiar person when hearing that person's voice compared to the voice of another familiar person. Further experiments using this cross-modal approach could clarify whether the ability for individual recognition is widespread across species. It is important to consider that failure to demonstrate individual recognition in a species using this cross-modal approach would not necessarily imply that individual recognition does not exist in that species. It is possible that individuals do not use the modality examined in the study to discriminate among individuals; for example, humans can recognize individuals but may fail this cross-modal test if olfactory signatures were coupled with visual or auditory signatures. Furthermore, if animals respond similarly to both congruent and incongruent situations, it is possible that they are capable of individual recognition but are responding to the novelty of the consecutive signals or cues.

Discussion

While individual recognition is important for social animals in discriminating among individuals, individual recognition does not exist in all species. One hypothesis explaining this variation in recognition is that animals

Table 1

Review of studies that have found evidence for individual recognition using a cross-modal approach

Order	Species	Multimodal assay	Recognition	Reference
Carnivora				
	African lion (*Panthera leo*)	Audio-visual	Conspecific	[48]
	Domestic dog (*Canis familiaris*)	Audio-visual	Hetero-specific	[49•]
	Meerkats (*Suricata suricatta*)	Audio-visual	Conspecific	[50]
Perissodactyla				
	Domestic horses (*Equus caballus*)	Audio-visual	Conspecific, Hetero-specific	[51,52,53]
Passeriformes				
	Large-billed crow (*Corvus macrorhynchos*)	Audio-visual	Conspecific	[54]
Primates				
	Chimpanzee (*Pan troglodytes*)	Audio-visual	Conspecific	[55•]
	Grey-Cheeked Mangabeys (*Lophocebus albigena*)	Audio-visual	Conspecific	[56]
	Rhesus macaques (*Macaca mulatta*)	Audio-visual	Conspecific, Heterospecific	[57,58,59]
	Ring-tailed lemurs (*Lemur catta*)	Visual-olfactory	Conspecific	[60]

evolved recognition abilities at levels that meet their minimum recognition needs ('minimum needs' hypothesis) [5•,61,62]. For some species, class-level recognition is sufficient for their behavioral needs while other species may need individual recognition. For example, swallows (*Stelgidopteryx serripennis* & *Hirundo rustica*) that do not nest in large colonies fail to recognize their young, which does not likely have negative fitness effects because of low nesting density [61]. Another hypothesis is that animals' recognition abilities are related to their general learning abilities via pleiotropy ('generalized learning' hypothesis) [5•]. Animals that use complex learning in other contexts, such as foraging or navigation, may be able to extend these abilities to recognizing individuals at levels beyond their minimum recognition needs. Alternatively, the environment may limit recognition abilities ('environmental constraint' hypothesis) [5•,63]. Animals living in complex environments may not exhibit individual recognition because their signatures are so degraded that it is impossible for them to discriminate among signalers [63]. Additional studies that document the existence of individual recognition across species that differ in their recognition needs, cognitive performances in different contexts, and environments will help us understand variation in recognition across taxonomic groups.

Conflict of interest statement

Nothing declared.

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