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Selective attention as a contributor to negative frequency dependent selection in predator–prey interactions

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It is proposed that selective attention may be a contributor to negative frequency dependent selection in predator–prey interactions. When predators use search images to identify prey, low-frequency morphs of those prey that do not match the search image benefit from their rarity. However, the use of search images may also be accompanied by some of the characteristic limitations of selective attention specifically connected to divided attention, conjunction searches and change blindness. Research on these aspects of attention from human cognitive psychology are reviewed and connected to search image use by predators. Some of the advantage enjoyed by low-frequency morphs may be enhanced by those flaws of selective attention. Furthermore, prey species may be able to further exploit those attentional limitations through specific behavioural strategies.

This article is part of the theme issue 'Exploring negative frequency dependent selection across levels: from genetics to ecology and back again'.

1. Introduction

Attention is an important determinant of behaviour in many animals. It allows for the preferential allocation of cognitive resources to the most appropriate targets in a complex environment. In an attempt to better understand this fundamental process, cognitive scientists have identified several ways that attention allows for the most effective allocation of those resources. Spatial attention for example, is preferential processing of information in specific spatial locations [1], as when a motorist monitors a busy intersection for oncoming traffic, or when a bird monitors its nesting area for predators. Object based attention involves allocation of attention to one or more objects in the sensory environment [2], independent of their spatial locations, as when an outfielder tracks a lazy pop fly as it rises and eventually falls into his glove, or when an owl tracks the motion of a scurrying mouse along the forest floor. Hierarchical attention allows one to adjust the scope of attentional focus to more local or global elements [3], as when a bird watcher switches from attending to a flock of birds to a single bird of interest, or when that bird adjusts its attentional scope from identifying the location of a pile of grain to selecting an individual seed within that pile. These and other attentional processes illustrate the complexity and usefulness of attention when navigating a complex world. While initially studied in humans, these cognitive processes have widespread relevance across a range of animals.

Attention is often characterized as a selection process that allows for some information to be preferentially processed. One of the earliest models of attention [4] for example, characterized attention as a filter that selects some information for further processing at an early stage, while other information is filtered out entirely. Selection is also a foundational theme in biology, as one of the central mechanisms behind evolution. Skinner [5] recognized

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the simultaneous importance of selection in behavioural and evolutionary sciences, and outlined the frequently overlooked parallels between *selection by consequences* and *natural selection* (as well as selection in the evolution of cultures). Selection by consequences is a mechanism by which an individual organism's behaviours are selected from the population of all possible behaviours based on the consequences that follow them. Reinforcing consequences increase the likelihood of a behaviour in the future, while punishing consequences decrease it. Skinner argued that both selection by consequences and natural selection are driven by consequent events (contingencies of reinforcement and punishment, or survival and reproductive success, respectively). Under some circumstances the selecting consequences are the same, and the two may be complementary. However, when the environment changes, learning via operant conditioning becomes an important addition to evolution [6,7].

A further parallel between selection of behaviours at the organism level (for example via reinforcement, in the case of selection by consequences) and selection of traits across generations (for example via differential survival, in the case of natural selection) is that the processes by which selection happens can vary. Reinforcement, for instance, is a fundamental learning process by which a behaviour is made more likely [8]. However, there is variability in the ways reinforcement can happen. Both positive reinforcement (presentation of an appetitive stimulus following a behaviour) and negative reinforcement (removal of an aversive stimulus following a behaviour) are important contributors to selection by consequences, and both result in a behaviour becoming more likely [9]. Natural selection is surely also owing to multiple processes. One of these is frequency dependent selection, in which the fitness of a phenotype or genotype varies depending on how common it is on a population [10,11]. Coincidentally, like reinforcement, frequency dependent selection comes in positive and negative varieties. In positive frequency dependent selection, fitness increases as a trait becomes more common. Individuals of an aposematic species hold an advantage if they have the same appearance as most members of their species. For example, poison frogs' (*Dendrobates pumilio*) toxicity is signalled by their colour, and birds which learn that association based on one encounter can apply it by avoiding other frogs that sport the same coloration [12]. Similarly, the colour patterns of chemically defended butterflies influence the frequency of attacks, with predation attempts decreasing as the local frequency of a colour pattern increases [13]. In negative frequency dependent selection on the other hand, the fitness of an individual with a specific feature increases as a feature becomes relatively more rare. An example of negative frequency dependent selection is seen in the rewardless orchid (*Dactylorhiza sambucina*), which produces either yellow or purple flowers. The fitness of each colour morph declines with its relative frequency because potential pollinators associate the colour with lack of reward, based on more frequent rewardless encounters [14].

To investigate the possibility that polymorphism could be maintained by negative frequency dependent selection, Madsen *et al.* [15] followed a population of adders (*Vipera berus*) for 37 years. The two distinct colour morphs varied from year to year, in a manner consistent with negative frequency dependent selection, and they conclude that as one of the morphs increased in frequency, it faced increased predation. In this manner, negative frequency dependent selection is one possible mechanism for maintaining phenotypic and genetic diversity within a population. Nevertheless, other processes (such as directional selection or density-dependent selection) may also contribute to maintenance of genetic variation that should not be confused with negative frequency dependent selection [16].

2. Search images as selective attention

Attention may contribute to frequency dependent selection via animals' use of search images during foraging or hunting. Predators tend to specialize in common forms of prey, and those common prey types make up a disproportionate number of captures. It has been proposed that predators accomplish this by forming an image of the most abundant prey item in their environment [17]. This search image allows them to quickly identify and select prey that match that image. Evidence for the use of a search image includes a bias to capture larger numbers of the most abundant prey types, in proportions even greater than would be expected based on their plentiful representation in the population. The strength of this effect is influenced by multiple factors such as morph coloration and distinctness, number of morphs, palatability, conspicuousness and density [18]. Furthermore, the bias increases with repeated encounters, and changes along with seasonal variation in prey frequencies, indicating that the search image used is at least in part, a product of learning [19]. Search images are presumably useful because there is a limited capacity to attention [20]. The amount of sensory information taken in cannot all be processed equally, and so some information must receive preferential processing. Search images allow an animal to select the information that is most likely to be useful. An alternative view is that even if attention is not limited, some information is more useful and relevant to immediate goals [21]. This competing perspective would still lead a similar conclusion, that search images allow for the most useful information to receive preferential processing.

A detailed understanding of how search images work has been provided by laboratory research. Reid & Shettleworth [22] investigated pigeons' (*Columba livia*) use of search images in the laboratory, by having birds search for different grain types on a gravel background. Grains of different colours were presented in different proportions across sessions, and pigeons showed a search image effect, consistently overselecting the most common colour, at a frequency even greater than the proportion presented in the condition. Birds also showed trial-by-trial effects, giving some insight into the cognitive processes that contribute to search images. Experience on one trial biased a bird towards selection of the same grain type on subsequent trials. Note however, that this result is consistent with either an attentional account (by which the selection and processing of some features is enhanced) or a purely learning based account (by which an animal gains a preference for, or increased handling skill specific to, some kinds of prey). However, the two can be distinguished in that an attention-based account would also predict that overselection should be more pronounced under cryptic conditions relative to conspicuous conditions, which would not require attentional focus.

Langley *et al*. [23] used a similar approach to further investigate that potential importance of context and crypticity. They presented coloured grains in either a cryptic context (a multicoloured tray) or a conspicuous context (a grey tray). As predicted, only in the cryptic condition were high frequency seeds overselected. In the conspicuous condition, all seeds were quickly identified and consumed at equal rates. Furthermore, a brief delay was sufficient to deactivate a specific search image, indicating that the search image was experience-dependent. These examples of laboratory research on selective attention demonstrate frequency dependent predation, in that potential targets with common features (ones that match the search image) are at increased risk. Uncommon morphs by contrast, are less likely to be captured. Importantly, the effect was dependent on and changed in different contexts, indicating a flexible, attention-based process rather than an evolved preference. While these laboratory investigations show search image use, and predation dependent on the relative frequencies of prey items, they do not necessarily lead to the conclusion that the population of prey are under frequency dependent selection, since there was no measure of changes to the prey population.

To investigate how use of search images might affect prey populations, Bond & Kamil [24] took a similar, laboratory-based approach, but added in a virtual ecology. Their blue jays (*Cyanocitta cristata*) foraged for digital moths displayed on computer monitors. Visual features of the moths varied within the virtual population, and undetected moths were more likely to reproduce and have their features appear in the next generation (e.g. subsequent experimental sessions). Results indicated that jays were less likely to detect atypical cryptic moths than typical ones, and over generations, moths showed increased phenotypic variance and became harder to detect. Importantly, these results suggest that frequency-dependent predation, as happens with the use of a search image could result in negative frequency dependent selection on the prey population. However, note that this experiment features a number of constraints that could be important: prey were digital images presented on a computer monitor in a laboratory environment, and successive generations were based on predatory behaviour of individual animals, rather than on the cumulative effects of a population of predators. Thus, one should be careful not to assume that use of search images would always lead to negative frequency dependent selection.

Search image effects like these are not limited to the laboratory, and appear all across the animal kingdom, using a variety of methods. They have been shown in many animals including blackbirds (*Turdus merula* [25]), blue jays (*Cy. cristata* [26]), kestrels (*Falco tinnunculus* [27]), sea otters (*Enhydra lutris* [28]), bumblebees (*Bombus fervidus* [29]), butterflies (*Battus philenor* [30]), spiders (*Evarcha culicivora* [31]), yellowfin tuna (*Thunnus albacares* [32]), skunks (*Mephitis mephitis* [33]), trained explosive sniffing dogs (*Canis familiaris* [34]) and rattlesnakes (*Crotalus viridis* [35]).

While the use of search images in a variety of predators has been well documented, as has the maintenance of genetic diversity in prey, a general, causal connection between the two is not a necessary conclusion. Results consistent with negative frequency dependent selection have been produced based on laboratory tasks using virtual prey [24]. However, these findings may not necessarily translate into frequency dependent selection at a population level. Most laboratory experiments analyse the behaviour of a small number of individual predators. A population of predators, in contrast, does not consist of a collection of individuals all behaving in the same way. Each will have a very different history of experience with prey frequencies, and that random variability would presumably weaken an overall frequency dependent selection effect. Furthermore, simulations of frequency dependent predation show that factors such as predator population size, prey population size, prey crypsis and prey discriminability can influence whether prey polymorphism is maintained [36]. Of particular importance, Merilaita [37] found that increasing the number of predators decreased the persistence of prey polymorphism, calling into question whether behavioural experiments on small numbers of individual animals would reliably translate into a population level effect. Similar simulation work highlights the importance of habitat heterogeneity [38]. Again, the conclusion is that frequency dependent predation can support polymorphism, but under specific conditions defined by factors such as habitat features and predator mobility. These results suggest that maintenance of polymorphism is affected by multiple variables related to search images. To the already identified external factors, we might consider internal cognitive processes such as attention itself.

Flexibility is one indicator that search image effects may be a consequence of predators' use of attention, and do not reflect a static preference for a specific prey type. Use of different search images, for example, can be primed with various methods on a trial-by-trial basis [20,39]. This part of the predator/prey dynamic is asymmetrical in that while predators can shift their attentional focus quickly, potential prey responses are more limited. The phenotypic features that might be part of a search image (such as shape, size, colour or texture), are either fixed, or at best less malleable than a predator's search image. For example, colour change can serve as a mechanism for camouflage in a wide range of animals [40] and might be an effective countermeasure against search images. However, colour change appears in only a limited number of species, and the time scale for colour change (ranging from seconds to months, depending on the species) is much slower than the time scale for attentional shifts (usually on the order of milliseconds). Furthermore, use of colour change to counter frequency-dependent predation would also require some additional cognitive load: prey would need to have a relatively accurate estimate of prey colour frequencies and the ability to respond as those frequencies change. These asymmetries would seem to confer a relative advantage to predators over prey. Nevertheless, attention does come with some inherent limitations, and these limitations may give prey some other ways to combat predators' use of search images, by exploiting some of the inherent constraints of selective attention.

3. Limitations and failures of selective attention

While flexible attention has useful features that can lead to success in predators, it is also subject to some notable limitations. Among these are decreased effectiveness under conditions requiring divided attention, and when searching for conjunctions of features. Furthermore, animals are subject to surprising failures of attention such as change blindness [41] under some conditions. Research into these specific limitations of attention from cognitive psychology provides some possible accounts for how prey species can counter predators' use of selective attention-based processes such as search images. These counter-responses may have some interesting consequences for negative frequency dependent selection.

(a) Conjunction searches

Different varieties of visual attention (spatial, object-based, hierarchical, etc.) exist to suit different situations. This variability implies that not all attention-based searches are equal: Some are more difficult than others in a particular context, and require more effort or produce lower accuracy. The salience of a feature for example, can have a powerful effect on detection [42]. A salient feature such as one that is brighter, larger or more contrasting will be more conspicuous and likely to be detected. Most searches in a complex world though are likely to include multiple features, and so the salience of individual features by themselves is an incomplete account.

Cognitive psychology has explored the differences between searches based on a single feature and those based on multiple features. Feature Integration Theory [43] proposes that perception involves qualitatively different early and late stages. In the early, pre-attentive stage, individual features of objects are separately and automatically processed. In the late, focused attention stage, those features can be combined into an integrated perception of the object. This relatively simple theory makes specific and meaningful predictions about the effectiveness of different kinds of searches. A feature search that requires attention to a single feature such as shape, colour, size or orientation can be handled by the early stage, and is thus done quickly and in a parallel fashion that is unaffected by set size. Response times under such conditions are uniformly fast, regardless of the number of potential targets or distractors. A conjunction search on the other hand requires attention to more than one feature at the same time. Conjunction searches require late-stage processing, and are thus slower and more effortful, and typically result in lower accuracy as well as slower response times. They are also affected by set size, with larger numbers of distractors yielding slower response times.

Figure 1 for example, shows a display of black circles and squares within a field of grey circles and squares (left panel). Identifying the odd region can be accomplished by a feature search, in that one can identify the odd region based on a single feature (colour) and ignore the other, irrelevantly varying feature (shape). The odd region 'pops out', and is seen easily quickly, regardless of the size of the search area. The right panel shows a display of grey circles and black squares amid a field of black circles and grey squares. Finding the mismatched region requires a conjunction search in that the odd region can only be identified by attending to how both features are paired. Accuracy is lower and response times are slower than searches that can be conducted based on a single feature. This conjunction search effect is not exclusive to humans and can apply in the same way to search processes in animals as well. Cook [44] trained pigeons (*Col. livia*) to peck odd regions of a visual display for food reinforcement. The odd region in each stimulus display was either defined by a single feature that was not present anywhere in the rest of the display, or by a conjunction of features, each of which was present elsewhere but not in the same unique pairing. Results were consistent with the same two-stage process suggested by Feature Integration Theory. Birds were more accurate and faster on feature searches than on conjunction searches.

Animal results on this topic are not exclusive to pigeons. Bichot & Schall [45] asked if macaque monkeys (*Macaca mulatta*) also showed conjunction search effects. They trained monkeys to make an eye saccade towards one of several visual displays, with the correct target defined either by a single feature or by a conjunction of features. Again, consistent with Feature Integration Theory, response times increased with set size on trials requiring conjunction searches, but not on trials requiring feature searches, suggesting that monkeys also use a similar two-stage attentional process.

The effect of conjunction searches even extends to animals with vastly different brain organizations. Reichenthal *et al*. [46] studied pop-out in archer fish (*Toxotes chatareus*), using targets that were defined by colour, size, orientation or motion. Fish showed a greater than chance selection of the odd target in each case, and furthermore, there was no effect of set size on response time. Fish were equally fast to select a target regardless of the number of distractors. When the target was defined by a conjunction of features, those results changed. Fish still selected the odd target at increased rates, but response time increased with set size, indicative of late-stage serial search.

While this collection of results suggest that this pattern might be a general feature of visual search, note that some animals do not show the standard pattern of search effects. Spaethe *et al*. [47] trained honeybees (*Apis mellifera*) to search for a coloured disc among varying numbers of differently coloured discs. Such a search based on a single feature would be expected to yield search times that are invariant of set size according to Feature Integration Theory. However, their bees showed increasing response times and decreasing accuracy with larger sets, suggesting a serial, not a parallel search. Here the difference could involve the interests of the search target. Whereas humans, pigeons, monkeys and archer fish may have search processes that seek a target that is better off if not found, the pollen sources that bees seek out have a common interest, perhaps making the early/late stage search processes an unnecessary elaboration for bees in this context.

A prey species with features that force predators to engage in a conjunction search should derive an advantage relative to one that can be detected using a feature search. Many prey animals seem to do just this by evolving specific physical features such as camouflage. Camouflage uses a range of adaptations that reduce signal-to-noise ratio and exploit perceptual processes for detecting features, edges, surfaces and objects [48].

One form of camouflage, crypsis, serves to prevent initial detection by a predator. In background matching [49], an animal is difficult to detect because it has a similar colour and pattern to the background. In disruptive coloration [50], an animal sports conspicuous features or patterns at the edges of its body, making its outline difficult to identify. While these are different forms of camouflage, both take advantage of a predator's early-stage attentional processing, and their effectiveness can be explained

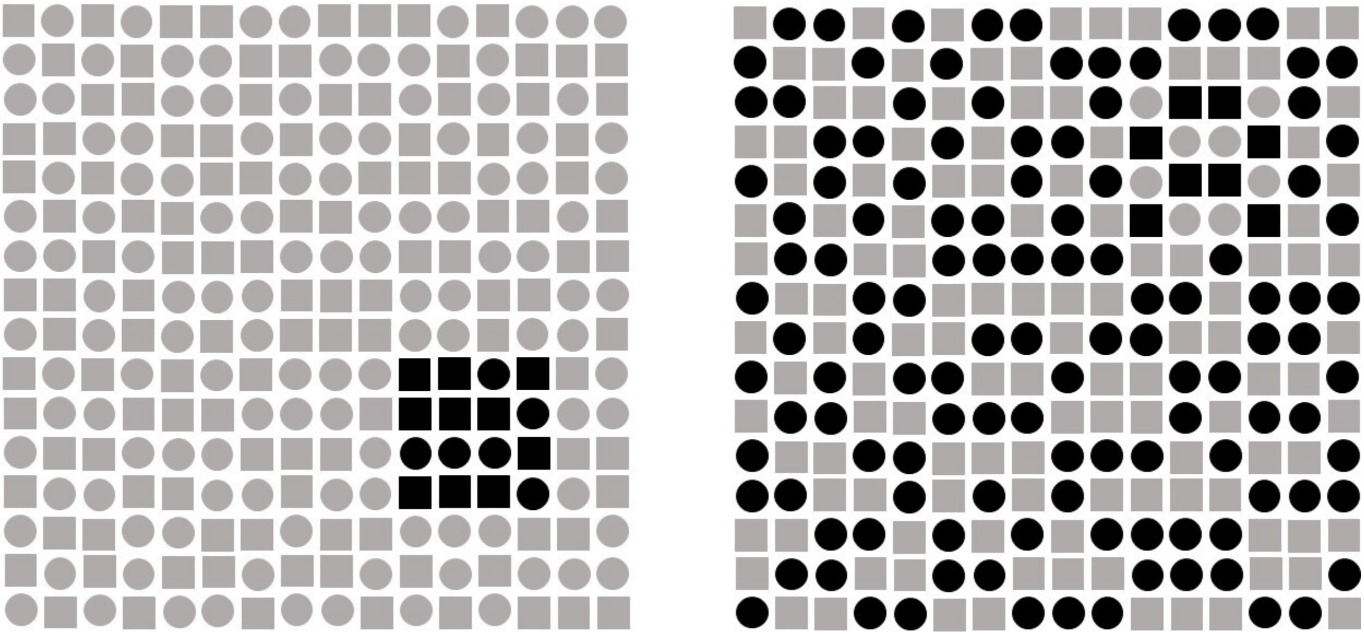

Figure 1. Example of stimulus displays requiring parallel and serial searches. The left panel features an odd region in the lower right quadrant defined by a single feature of colour. The right panel features an odd region in the upper right quadrant defined by a conjunction of colour and shape.

by Feature Integration Theory. In particular, they foil a feature-based search, either because the animal shares features with the background (background matching) or because salient features do not correspond to the target's actual edges (disruptive coloration). The consequence of either is that a predator cannot identify individual prey by using a fast, efficient feature search. Instead, they must search for a conjunction of features such as a specific combination of size and colour, which is slower and less accurate than a search for one of those features alone. Thus, genes for features that vary independently might carry some evolutionary advantage for prey species. In addition, morphs whose rareness is based on a conjunction of more than one feature would benefit not just from the its relatively low frequency in the population (standard negative frequency dependent selection), but also from the added challenge faced by a predator needing to use a conjunction search. This prediction assumes that other factors (such as level of camouflage) remain equal. The advantage derived from requiring a conjunction search could for example, be reduced or negated if the features in question make an animal more conspicuous.

An alternative form of camouflage is masquerade [51]. In masquerade, an organism closely resembles an inedible or otherwise inconsequential object. Within a Feature Integration Theory [43] framework then, masquerade happens at a late attentional stage, after the object has been selected and (mis)identified. The challenge for a predator in this case is not efficient search, but post-search discrimination learning. Indeed, predators can learn from experience to discriminate between masquerading prey and the objects they resemble [52]. Furthermore, the predation of masqueraders is frequency dependent in ways that would be predicted by Feature Integration Theory. Twig-mimicking caterpillars (*Selenia dentaria*) benefit less as the density of masqueraders to models increases [53]. Note that in this case it is frequency relative to models that is relevant, rather than frequency relative to other phenotypes. The effect on predators was owing to two factors: increased difficulty of detection, and decreased motivation to search for the masquerading prey type. The former factor lines up with Feature Integration Theory. The latter presumably reflects predators' ability to adjust their strategy based on reinforcement rate.

While masquerade derives its value by forcing less efficient late-stage attentional processing, it is also not incompatible with early-stage camouflage strategies such as background matching: in fact some prey might be able to take advantage of the two simultaneously, by resembling an inedible object, that also appears against a background of shared features. Further connecting the two, it has been suggested [51] that masqueraders may have evolved from cryptic ancestors. For predators, the required discrimination learning for dealing with masquerade can be easy or difficult, depending on the number of features required for effective discrimination and the match between target and distractor. Presumably at some point, the discrimination may become difficult enough that a predator is best off abandoning that target type and pursuing a different prey. Learning theories point out that discrimination learning is known to involve both excitatory and inhibitory processes [54], and these processes may have important by-products or consequences for discrimination learning. That is, the reinforced stimulus or S+ acquires excitatory value with training. At the same time, the non-reinforced stimulus or S− acquires inhibitory value. This suggests that the non-reinforced stimuli (i.e. models) may take on aversive value, especially with accumulating numbers of false alarms [55], and this would be expected to occur during masquerade, with frequent encounters with non-prey distractors as the S− acquiring inhibitory value.

Another defensive strategy closely related to masquerade is Batesian mimicry, in which a mimetic species closely resembles an unpalatable model species. Predators learn to avoid mimics based on encounters with models. Like masquerade, Batesian mimicry is assumed to be frequency dependent, and should be reduced either in the absence of the unpalatable model or when the mimic is relatively abundant. For example, non-venomous king snakes (*Lampropeltis triangulum alapsoides*) resemble venomous coral snakes (*Micrurus fulvius*), and predators learn to avoid attacking king snakes. However, avoidance of the mimic only happens in areas that are also inhabited by the model, implying that the ratio of mimics to models is important [56].

Furthermore, mimicry is another example in which predators adjust their foraging strategy based on economic factors. Just as a predator can switch search images based on changing frequencies of prey morphs, they may also change search strategies based on economic considerations such as prey availability, and required effort per capture. A cognitively demanding search process (like the conjunction search required to detect mimics or masqueraders) may not be worth the required effort if it yields only a small proportion of correct detections. In those cases, predators would be expected to switch to searching for a different prey type, that yields a higher proportion of correct detections or is less cognitively demanding (or both).

Just like predators, prey might also derive a benefit from adjusting behavioural strategies. In this case though, those strategies would be ones that exploit, rather than attenuate limitations in the predator's attention system. Obviously, a preference for a habitat that is either visually complex, or that matches one's own features (or both) would be beneficial for survival. Simply having features that qualify as camouflage (either crypsis or masquerade) are not maximally beneficial: one can further enhance their effectiveness by exhibiting a preference for environments where they will be most effective. Masquerading organisms for example, display complex microhabitat selection [53] that allows them to maximize protection from predation as well as food availability when both are available, or to change locations strategically in a way that increases overall gain when the two goals are incompatible.

Some possible lines of new research are suggested by research on conjunction searches, based on factors that affect the efficacy of visual search in humans. Koshino [57] for example, investigated excitatory and inhibitory processes in humans' visual search by repeating relevant features on consecutive trials. Excitatory processing would be revealed by faster responses when target features were repeated on consecutive trials. By contrast, inhibition would be revealed by slower response times when distractor features on one trial became target features on the next. He found that conjunction searches generally involve excitatory processes, regardless of set size. Inhibition on the other hand, was only found when set size was large. It seems intuitive that excitatory processing would be part of most animals' search image use, but less clear is the role of inhibition, which could be investigated in similar ways. If inhibition is involved, there are both behavioural and evolutionary implications. On a behavioural level, the point at which inhibition becomes involved would be of interest, as inhibitory processing has emerged as an important component of psychology, behaviour and neuroscience [58]. On an evolutionary level, there may be important survival-based consequences, especially for predators that must balance search behaviour with detection of their own predators. Thus, inhibition in that context could carry significant additional costs.

Further affecting conjunction search is the relative position of a target. Measures of performance in humans (both response latency and accuracy) are impaired if the target is located further from the initial point of fixation [59]. If animals are similar, there are easily derived hypotheses based on the size and shape of an animal's visual field, speed of travel during foraging, and frequency or magnitude of eye movements, among other variables.

(b) Divided attention

Attention is often considered in economic terms, as a limited resource that must be allocated strategically. As with any limited resource, allocation of attention to more than one target leaves less remaining for others. A classic example from human cognition is the cocktail party effect, based on the premise that when presented with multiple streams of information, such as the cacophony of parallel conversations during a crowded cocktail party, one can nevertheless filter out the irrelevant ones and attend exclusively one's partner's sparkling conversation about the dynamics of pigeon attention. Cherry [60] studied this phenomenon using a dichotic listening task, in which participants simultaneously listen to two different speech streams. Participants were easily able to listen to and understand one speech stream while ignoring the other. However, listening to both simultaneously was virtually impossible, and very little information was extracted from the unattended speech stream. Neisser & Becklen [61] obtained similar results in a visual version, in which participants viewed two superimposed videos at the same time. Again, selectively attending to one video was relatively easy, and participants were able to remember the contents of the attended, but not the unattended video. Attending to both came at a cost, and neither stream was remembered as well.

Animals too, show a cost to divided attention. To investigate divided attention in pigeons (*Col. livia*), Maki & Leith [62] conducted a matching to sample experiment with two different kinds of samples. On single element trials, the sample was a single feature, either a colour or a line orientation. Following the sample, comparison stimuli of the same type (colours or line orientations) were presented and birds were rewarded for pecking the one that matched the sample. On compound trials, samples consisted of two elements, a colour and a line orientation simultaneously, with no indication which would be relevant to the matching choice. Following the sample, comparison stimuli (either colours or line orientations) were again presented, and birds were rewarded if they pecked the element that was present in the compound sample. Compound trials therefore required birds to divide attention between the two elements of the sample stimulus, whereas single element trials did not. If there is a cost to divided attention, one would expect better performance on single element trials than on compound trials, and this is exactly what was found. Thus, it seems that dividing attention comes at a cost in pigeons, as it does in humans.

Again, this effect is not limited to one nonhuman species, and similar divided attention effects can be seen in other animals. Blue jays (*Cy. cristata*) detect cryptic prey more effectively when searching for a single prey type than when required to divide attention between searching for two different prey types [20]. In addition, attention can be divided across sensory modalities, with the same limited-resource effects. Rats (*Rattus norvegicus*) can perform a discrimination task requiring attention to either an auditory or visual stimulus. However, if attention to both modalities is required at the same time (requiring division of attention between the two), performance is impaired [63].

There are numerous variables that affect performance on divided attention tasks. One notable factor is the novelty of the target, which usually makes things more noticeable. For example, 'pop-out' effects occur when a novel stimulus appears within the context of a sequence of familiar stimuli. McCarthy & Reed [64] found that human participants were better able to remember pictorial stimuli that were from a different category than the rest of the stimuli in an array. A similar pattern is seen in the von Restorff [65] effect, in which there is better memory for distinctive rather than expected items.

Such pop-out effects based on novelty are also seen in animals. Ben-Tov *et al*. [66] presented archer fish (*To. chatareus*) with arrays of moving stimuli, one of which was moving in a different direction from the others. Fish were more likely to shoot at the mismatched target than would be predicted by chance. Furthermore, there was no effect of array size on response times, indicating that selection of the odd target is similar to the pop-out effects seen in humans, and indicative of parallel search.

However, the general pattern is sometimes reversed on tasks that require divided attention (Schmidt & Schmidt [67] propose a model that may account for the differences). Spence *et al*. [68] for example, found that response times to targets appearing in one of three modalities were slower when the target appeared in an unexpected modality, presumably indicating that those unexpected targets were less noticeable, and that attentional resources were divided across the monitored input channels. Similarly, spatial attention research often leans on a cue validity effect, whereby response times are fastest on valid trials, in which the location of an upcoming target is indicated by a probabilistic cue [1]. Invalid trials are rarer, but less noticeable, yielding slower response times. In these cases, novelty does not cause targets to pop out, but just the opposite: the novel target is less noticeable.

Again, this pattern is not unique to humans and can be seen in other animals. Recall that the general pattern of unexpected stimuli being less noticeable parallels the search image effects summarized earlier. As a further example, Croze [69] trained carrion crows (*Corvus corone*) to search for three kinds of painted seashells containing food. On days when only one colour of shell was presented, crows were more successful and obtained more food than on days when all three colours were present. In other words, there was no pop-out effect, and novel stimuli were not more noticeable, even after a run of captures of the same type. The same pattern of results is often used in comparative cognition, in the form of base rate priming effects. Fremouw *et al*. [70] for example, trained pigeons (*Col. livia*) to search for specific letters in hierarchical stimuli. Hierarchical stimuli consisted of large ‘global’ characters constructed from arrangements of smaller ‘local’ characters. Birds could be rewarded for pecking the left key when a letter H was present at either the local or global level, and for pecking the right key when a letter S was presented at either level. When presented with a global letter H, formed of local letters T, or a global letter E composed of local letters H, responses on the left key were reinforced, and if the H at either level was replaced with an S, responses on the right key were reinforced. After training, they presented birds with blocks of trials in which the majority (85%) of targets appeared at either the global or the local level. When they did, response times were faster for targets appearing at the primed level, and slower to targets appearing at the unprimed level. Again, it was not novelty, but expectation that made the target more salient.

This expectancy effect constitutes another likely connection between divided attention and processes that can lead to negative frequency dependent selection. Predators presumably select search images to use from a number of possible candidates, based on their expectations about the prey features they are most likely to encounter. Doing so would maximize their foraging success by increasing captures of the most common forms of prey. Note that this change in behaviour need not involve an intentional choice of search images (learning could be implicit; see [71]), and would be dependent on the predator’s perception of apparent prey frequencies, not necessarily the true frequencies (affected by sampling error, cryptic prey, etc.). While individual prey do not usually have the option to change those searched-for features, natural selection could result in changes to features over generations. In particular, the kinds of features that are consistent with pop-out effects in humans and other animals (based on salience, feature independence and novelty) would probably be selected against. Furthermore, any attention-based effects should be most prominent in predators that must also scan for predators of their own (requiring divided attention). More importantly, even in the absence of naturally selected features, individual prey do have some behavioural counter-strategies available. Prey might acquire behavioural strategies such as preferences for locations based on the frequencies of individual features or conjunctions of features in conspecifics. For example, migration from an area with a high proportion of shared features to one with a lower proportion could enhance survival of an individual because it would be less likely to match the search image of a predator in the new location. Even if such migration does not result in the individual now being rare, such migration could force a predator to divide attention between two different search images, which also carries an advantage for the prey. In support of this possibility, some polymorphic species arrange into geographical mosaics, with adjacent populations having different frequencies of morphs, despite their similar habitats [72]. The formation of these mosaics may be influenced by a variety of factors, importantly including predator perspective and prey movement [38,73].

Finally, simply migrating based on overall population density (either high or low) could be an effective strategy. Dispersal to an area of low density could reduce predation if predators are drawn to areas with large numbers of prey. Hammill *et al*. [74] demonstrated that such an effect exists, but also that it reverses above a specific threshold of prey density, leading to aggregation. Thus, both dispersal and aggregation can be effective strategies, depending on the context. Migration to a higher density area could further benefit an individual via the ‘confusion effect’. This effect is the tendency for larger prey groups to lead to more attacks per kill, and is presumed to be a consequence of increased difficulty of singling out individual targets [75]. This presumably reflects a trade-off between increased risk of detection and decreased risk of selection. A larger group is likely to be more conspicuous than a smaller one. However, if individuals within the group must be targeted, detection may be accompanied by a reduced risk of selection and overall reduced mortality. The contrast between detection and targeting resonates with the results of early stage (feature-based) and late stage (conjunction) searches, respectively. The former would be assumed to require few attentional resources, relative to the latter. However, both are required for a successful capture. Landeau & Terborgh [76] demonstrated the confusion effect in largemouth bass (*Micropterus salmoides*) predation of silvery minnows (*Hybognathus nuchalis*). Bass effectively captured individual minnows, but their efforts were rendered ineffective when minnows numbered eight or more, despite the increased number of targets. Furthermore, inclusion of one or two blue dyed minnows among the group attenuated the confusion, increasing bass’s ability to capture prey from among a group. A further application of divided attention is the necessary trade-off between foraging and vigilance that many animals must balance the two [77].

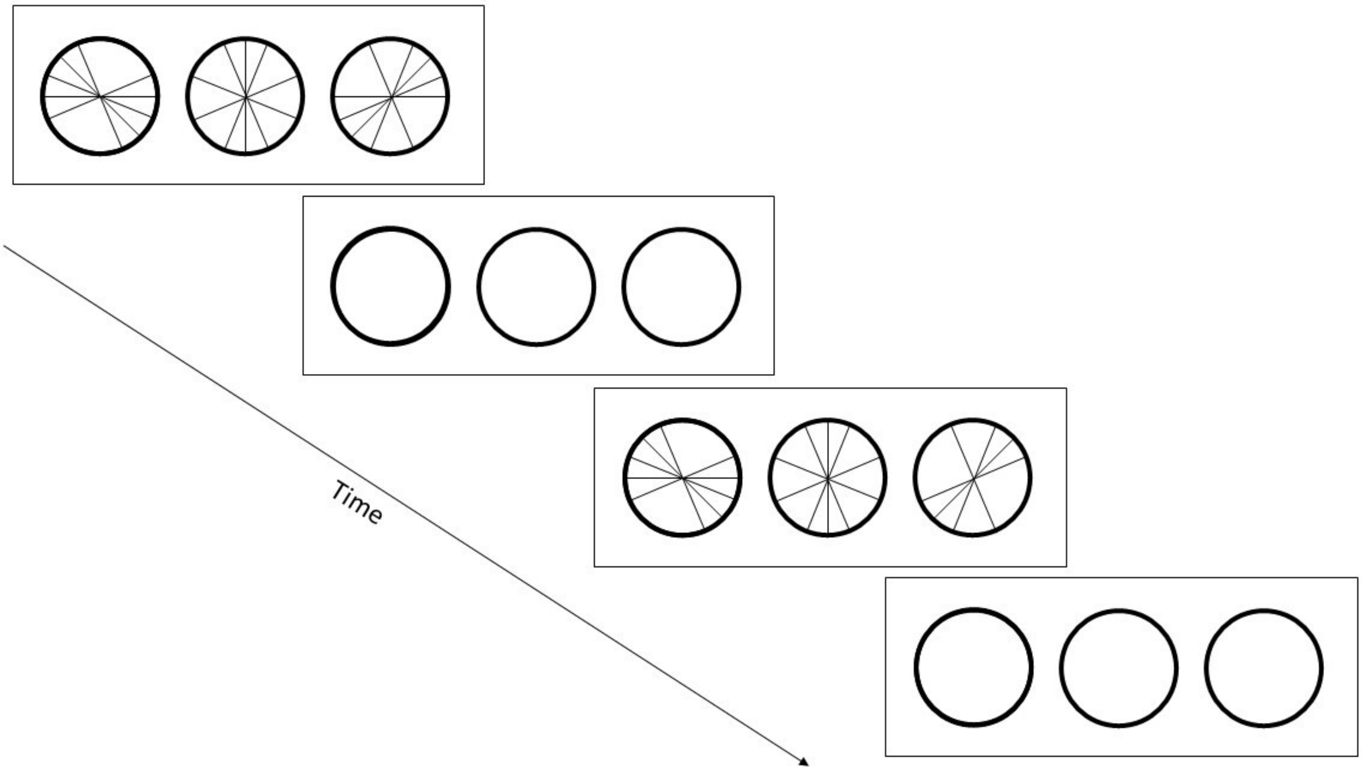

Figure 2. Example of a stimulus display in a change blindness experiment. The two displays featuring lines in the first and third positions are the same except for a single feature (the horizontal line on the rightmost key). Change blindness is dependent on the blank stimuli in the second and fourth positions corresponding to the ISI. When the ISI is omitted, changes are easier to identify.

Again, there are some suggestions for possible lines of research inspired by contemporary human cognition research. With sufficient practise, humans can surprisingly move beyond the frequently assumed limits of attention. For example, Spelke *et al.*'s [78] participants (after some weeks of practice) were able to write words and categorize words for meaning, while reading for comprehension at a normal speed. Untrained individuals fail spectacularly at such attempts, suggesting that the characterization of attention as a fixed resource may be overstated or outright false. Most animal research on divided attention requires some degree of training, but probably not to an extent that would parallel that undergone by Spelke *et al.*'s participants. Nevertheless, there are consistent effects of overtraining in animal learning, including faster reversal learning, and improved generalization [79]. Whether such effect extend to foraging via search image, or at what point overtraining effects are seen would have important implications for negative frequency dependent selection.

(c) Change blindness

In addition to static visual features, predators can use other signals to identify prey, such as motion or change. While change detection is useful, recent research shows that it also is not without inherent constraints. Rensink *et al.* [80] developed a 'flicker task' to study change detection in humans. They presented participants with two photographic images that were identical with the exception of a single localized change. The stimulus display switched between the two images repeatedly, and participants were simply asked to identify the change. If the transitions between images were instantaneous with no time delay or interruption, they did so quickly and accurately. However, if images were separated by a brief inter-stimulus interval (ISI), during which the display was blank (producing the flickering effect for which the procedure is named), accuracy dropped and response times slowed. This kind of change blindness is not just a low-level physiological effect, as it can be influenced by experiences and expectations. Rensink *et al.* found that changes of central importance (those involving the primary subject of the image) were more likely to be identified, even in the more difficult condition. Werner & Thies [81] further found that subjects who were experts in American football were better able to detect meaningful changes to football scenes than non-experts, another instance of influence by experience and expectations. This finding resonates with predators' use of search images, in that participants were able to identify some searched-for changes based on their expectations (akin to use of a search image), and that they missed some changes (akin to cryptic prey) that did not match their expectations. In addition, expectations can be manipulated in a change blindness experiment, and this affects the likelihood of detection. For example, if a scene depicts an individual looking at the change, the change blindness effect is attenuated and participants are more likely to correctly identify the change [82]. This confirms that like other attentional phenomena, change blindness can be manipulated by adjusting task details via techniques such as cueing, and therein lies its value as a research tool.

Herbranson *et al*. [83] developed a pigeon version of the flicker task meant to parallel that of Rensink *et al*. [80]. Pigeons (*Col. livia*) viewed alternating displays of up to 24 lines across three response keys. Alternating displays were the same, save for the addition or deletion of a single line on one of the three keys, and birds were reinforced for pecking the key that coincided with the change. As in the human implementation, some trials featured an ISI between displays, during which the keys were blank, and others did not. Figure 2 shows an example of a stimulus display with the ISI.

They found a change blindness effect parallel to that seen in humans, in that accuracy was worse when successive displays were separated by a brief ISI during which the keys were blank. In addition, accuracy increased as the number of repetitions presented increased, and patterns of responding indicated that pigeons used a serial search strategy, beginning at one response key and proceeding to the next only if a change was not detected. Further research using the same paradigm parallel human change blindness results, including effects of change salience and timing [84]. The same change blindness effect has also been demonstrated in rhesus macaques (*Ma. mulatta*), using a parallel procedure [85]. In addition to the primary change blindness effect in which accuracy is worse on trials with an ISI, they found that the change blindness effect could be attenuated if the location of an upcoming change was cued in advance.

The phenomenon of change blindness may be relevant to negative frequency dependent selection as another weakness of selective attention that might favour rare prey types. Predators would be expected to miss movements of low-frequency morphs more frequently than common ones because of the experience and expectation effects demonstrated in change blindness research. Furthermore, prey respond to subtle indicators of risk that may be less noticeable than an obvious looming predator. For example, head orientation and gaze direction of predators are easily seen and can be reliable predictors of risk. Carter *et al*. [86] showed that European starlings (*Sturnus vulgaris*) were sensitive to orientation and gaze direction of humans, and responded appropriately: when gaze was averted, starlings resumed eating earlier and ate more quickly. A subtle but reasonable elaboration on this ability could be the ability to identify moments congruent with the real-world triggers of change blindness, such as eye saccades, blinks and gaze shifts. Some animals may even be able to initiate change blindness in predators based on their own behaviour. Flash behaviours (or deimatic displays) are produced in response to approach by a predator, and involve sudden display of a conspicuous but previously hidden trait [87]. It has been proposed that flash behaviour is an escape mechanism that impairs a predator's ability to effectively track prey as they move and change position. This would benefit any prey animal, but would be especially useful to rare morphs in that they would already be more subject to benefit from predators' change blindness based on their rarity.

Again, there are some potential lines of research that naturally emerge from the literature on human cognition. While the methods that have been used to study change blindness in animals might not be easy to directly apply to a search image-based foraging scenario, they do demonstrate the relevance of the phenomenon to nonhuman animals. Other demonstrations of change blindness do not involve visual disruption or rapid presentation of stimuli [88]. Thus, other implementations of change blindness that better match the use of search images would be informative. Perhaps the most fascinating aspect of change blindness is the refusal to acknowledge its effect on one's own perception, dubbed 'change blindness blindness' [89]. This phenomenon would have important implications on an animal's ability to accurately estimate frequencies of items (such as prey in an environment). Such misestimations would have important consequences on frequency dependent predation, in that changes to predatory behaviour are based on the predator's (accurate or inaccurate) estimation of those frequencies.

4. Relevance of attentional processes to negative frequency dependent selection

These three very general limitations of attention (conjunction search, divided attention and change blindness) that exist in a wide array of animals might contribute importantly to some subtle but important patterns in negative frequency dependent selection. The purpose of this paper has been to connect negative frequency dependent selection in predator–prey interactions with contemporary research in cognitive science, as the two research communities may not be aware of each other's relevance. Much of cognitive psychology emphasizes the proximate causes of behaviour, overlooking the ultimate causes and evolutionary significance. At the same time, evolutionary research may focus on animal populations without awareness of relevant developments in cognitive science. Laboratory research in comparative psychology has shown that multiple species show attention effects whereby visual search is impaired under conditions of divided attention relative to selective attention. Similarly, animals take longer to identify targets when they are designated by a conjunction of features rather than by a single feature. Also finally, several species are subject to change blindness effects and may miss an otherwise conspicuous target entirely when visual continuity is disrupted. Some of these may be unrecognized contributors to negative frequency dependent selection in that they are enhanced in novel or unexpected targets: change blindness is more likely when the change is unexpected, and divided attention can lead to missed targets, especially when those targets are rare. Furthermore, these attentional flaws open up some behavioural strategies (such as strategic migration based on conjunctions of features in a population, participation in confusion effects, or attention to predators' gaze and eye movements) that could be used by prey to enhance the benefits gained from negative frequency dependent selection.

To conclude, the use of search images by predators may reflect the use of cognitive processes that contribute to negative frequency dependent selection in predator/prey interactions. If we consider the features of selective attention as the likely foundation of search image use, we can identify some important patterns within the phenomenon, and potentially even gain a more complete understanding of both the proximate and ultimate causes of attention dynamics in animals.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. This article has no additional data.

Declaration of AI use. I have not used AI-assisted technologies in creating this article.

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