Supernormal Stimuli and Responses

T N C Vidya

In this article, I describe the curious phenomenon of exaggerated responses to supernormal stimuli in animals. These have been observed across various taxa and include preferences for larger egg size, darker or more contrasting colours or, in the case of humans, preferences for processed foods and television among others. I describe mechanisms that have been proposed to explain supernormal responses and possible consequences of such responses.

T N C Vidya is interested in animal behaviour and phylogeography, and teaches these at JNCASR. Her primary research is on the social organization and behaviour of Asian elephants.

Keywords
Supernormal stimuli, sign stimuli, exaggerated response, Nikolaas Tinbergen, oystercatcher egg size, food-begging in gulls, grayling butterflies, generalization and peak shift, brood parasite.

Experiments with Oystercatchers and Other Birds

The Eurasian oystercatcher (*Haematopus ostralegus*) is a wading bird that feeds on earthworms and mussels. During a study of this oystercatcher, ethologist Nikolaas Tinbergen (see articles by Sindhu Radhakrishna and Raghavendra Gadagkar in this issue) noticed that female oystercatchers laid a few eggs and then began to incubate the entire clutch. Tinbergen and his colleagues presented female oystercatchers with a clutch of five eggs rather than their normal three eggs and found that they preferred to incubate the larger clutch that was not their own! The scientists proceeded to offer the females a choice of eggs of varying sizes. In most cases, the females clambered on to the largest egg, which was many times the size of their normal egg, making it extremely difficult for them to even sit down upon [1] (see *Figure* 1)! Similar experiments were carried out in herring gulls and black-headed gulls by removing the gull's eggs when the bird was away from the nest and placing two eggs at the rim of the nest. Gulls have a tendency to retrieve eggs that have rolled away accidentally and would, therefore, choose one of them first to roll back to the nest, exhibiting their preference. Using different combinations of artificial eggs, Tinbergen and his colleagues showed that gulls also preferred larger eggs to smaller ones. You can, perhaps, try this

Figure 1. **(a)** Eurasian oystercatcher at the nest. Photo by John Haslam. Source: https://en.wikipedia.org/wiki/Eurasian_oystercatcher#/media/File:Haematopus_ostralegus_-Scotland_-nesting-8.jpg under Creative Commons license CC BY 2.0. **(b)** Oystercatcher preferring giant egg to its own (smallest) egg. Source: Artwork by T N C Vidya based on *Figure* 43 from Tinbergen [1].

experiment with pigeons, ducks or hens! Reactions to stimuli from artificial eggs in the context of colour, not size, had first been described by Koehler and Zagarus in an article (unfortunately, for us, in German) on the ringed plover in 1937. Koehler and Zagarus found that the plovers preferred eggs with clear white background and black spots to their own light brown eggs with darker brown spots.

Why did these birds prefer artificial eggs to their own eggs, especially when the artificial eggs were of a size that they could not have possibly laid themselves? The large egg size and marked colour contrast above are examples of what are referred to as 'supernormal stimuli'. As the term suggests, supernormal stimuli are exaggerated versions of stimuli to which animals respond more intensely than to normal stimuli. While the preference for a slightly exaggerated version of the stimulus may be adaptive – for instance, preference for a larger egg over a smaller egg within a normal range may be beneficial as larger eggs may be more viable – the supernormal stimulus hijacks the normal, possibly adaptive, response and leads to an exaggerated or supernormal response.

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Apart from his work on the organisation of instinctive behaviour or 'fixed action patterns' – behaviour that is largely influenced by genetic rather than environmental components and is, therefore, shown by animals in response to a specific stimulus without any prior experience – Tinbergen is famous for his work on supernormal stimuli. The stimuli that evoked instinctive behaviours were called 'sign stimuli' or 'releasers' (as behaviours were thought to be released by an 'innate releasing mechanism' by Konrad Lorenz, who first suggested this idea). Tinbergen observed various animal behaviours to identify releasers of those behaviours (see Sindhu Radhakrishna's article in this issue for a description of Tinbergen's work on sticklebacks). One such behaviour was 'food-begging' by chicks of herring gulls. Using models of herring gull heads with various combinations of head, bill, and bill patch colour, head shape, bill length, and movement, Tinbergen and Perdeck [2] found that herring gull chicks pecked most at moving cardboard cutouts with long bills, whose bill patch colour contrasted with that of the bill. Herring gulls have a white head, yellow bill, and a red bill patch. Tinbergen and Perdeck then presented chicks with a choice of a thin, red rod with three white bands at one end, and a three-dimensional head, and found that the former seemed to be perceived as a 'supernormal bill' and was preferred to the latter.

Supernormal Stimuli in Other Taxa

Tinbergen showed that the grayling butterfly also reacts to supernormal stimuli, in the context of finding a mate [3]. Male grayling butterflies are seen resting camouflaged on the ground or tree barks and flying up towards passing females. Females respond by alighting upon the ground if they are ready to mate, or by flying away if they are not, upon which the male would abandon the chase and settle down to wait for another female. Interestingly, males were sometimes seen flying up towards falling leaves, other butterflies and insects, birds, and even shadows! Using paper dummies tied to a stick and various combinations of characteristics such as colour, size, and shape, Tinbergen and his colleagues carried out about 50,000 tests on male graylings in the wild and found that black dummies elicited a greater response from males although females were naturally brown. Larger dummies were also important, as was fluttering movement, although the shape was not. Simple circles or rectangles could elicit the same response as a butterfly-shaped dummy! Thus, larger, darker, flying dummies seemed to provide supernormal stimulation. Why would males waste their energy flying up towards objects that are not conspecific females? If females were rare and/or competi-

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tion amongst males for access to females important, the cost of reacting to other objects (energetically and/or through possible exposure to predators) might be outweighed by the benefit of not missing flying females, and therefore, increasing the male's reproductive success. Similarly, Australian jewel beetles have been found attempting to copulate with shiny, brown beer bottles that seem to be perceived as supernormal females [4], a finding that earned Gwynne and Rentz the Ig Nobel Prize in 2011!

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Are humans sensitive to any supernormal stimulus? A quick look around leads to a resounding YES. An everyday example is the craving for various processed foods, optimised to provide our taste buds with irresistible combinations of sugar, salt, and fat that natural foods seldom possess. Supernormal stimuli are also evident in depictions of the human body in paintings and sculpture to appear more sexually attractive. Movie superheroes, certain video games, television shows, and social media are also thought to provide supernormal stimuli, exaggerating social stimuli that are normally beneficial. Hyperbole in language presumably serves the same function.

Mechanisms for Supernormal Response Generation

How do supernormal responses arise? Research during the 20th century showed that certain principles seem to be followed in generating learned responses to stimuli. The first, called 'generalization', is that novel stimuli evoke the same response as established behaviour towards known stimuli if the two stimuli are similar. There is a gradient of generalization such that the response to the novel stimulus decreases with decreasing similarity of stimuli. The second, called the 'peak shift', is that modified stimuli can sometimes elicit a more intense response than expected, in a specific direction. For example, if an animal is trained to discriminate between the colours red and orange by providing a reward when it chooses red and no reward when it chooses orange, red is a positive stimulus (S+) and orange is an inhibitory (S-) stimulus. Each has a gradient of generalization around it,

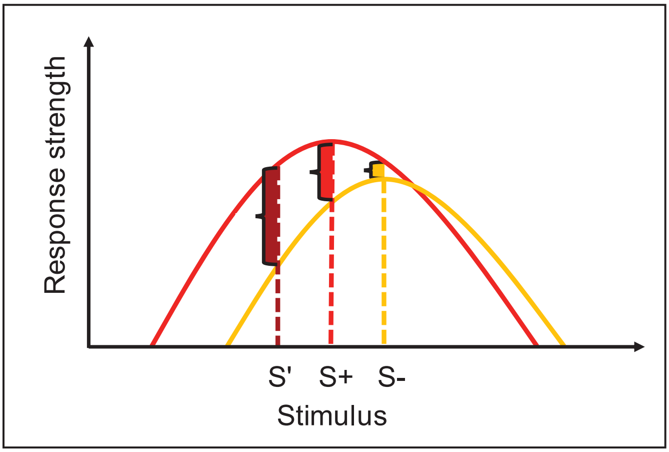

Figure 2. Gradient of generalization and peak-shift illustrated. S+ (red colour) and S- (orange colour) are two stimuli that an animal is trained to discriminate between by providing a reward when it chooses red and no reward when it chooses orange. Each stimulus has a gradient of generalization around it, represented by the two curves. The excitatory generalization gradient (around S+) is larger than the inhibitory generalization gradient (around S-) because of reward-associated learning. S' (dark red) is a new stimulus presented to the animal. The difference between the two gradients, shown as filled set brackets, results in the tendency to approach one stimulus versus another. The animal prefers S' instead of S+ that it had earlier been rewarded for because the magnitude of difference between the gradients is greater at S' than at S+. Drawn after Pearce [5].

the responses around S+ being more frequent than that around S- because of reward-associated learning. Now, if a new stimulus (S') is presented to the animal in the form of dark red colour, the animal prefers dark red (S') instead of red (S+) that it had earlier been rewarded for because the magnitude of difference between the excitatory (S+) and inhibitory (S-) generalization gradients is greater at the dark red stimulus (S') rather than at red (S+) itself (*Figure* 2, see [5]). This, then, could result in exaggerated responses such as to supernormal stimuli. Peak shifts occur during discriminant learning and should not themselves be confused with supernormal responses, but it is possible that there is a similar mechanism in the latter, with an underlying bias (such as a 'bigger is better' rule) having been shaped adaptively over evolutionary time. This underlying bias is possibly shaped by asymmetric selection pressure, corresponding to differential reward in the learning paradigm above. It has been suggested that just as there is a reward ('selection') for a specific preference but no punishment for the other in the learning experiments, there might be selection for, say, large eggs as opposed to small eggs, but no selection against supersized eggs, leading to the underlying bias [6]. This is, obviously, not always the case, as there might be other costs such as predation.

In 1993, Enquist and Arak used a simple neural network model to try to explain the evolution of exaggerated signals and suggested

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that the evolution of hidden biases was inevitable in recognition systems. This study was criticised as the simple neural network model used probably did not represent animal recognition systems, and a subsequent study to address a similar problem did not find evolved networks to be responsive to supernormal stimuli. In more recent times, while neural network models have become more complex, how well they can predict supernormal responses remains to be seen. In terms of a mechanistic neurobiological understanding, studies in humans have suggested that dopamine plays an important role in learning and in reward pathways, thus motivating (adaptive) responses towards stimuli. Supernormal stimuli in humans are thought to act as addiction-forming substances, making the individual seek out more of the stimuli. This can eventually lead to dopamine desensitization, with more and more stimuli required to elicit a response.

Evolutionary Significance

What are the evolutionary outcomes of exhibiting supernormal responses? As mentioned above, supernormal responses usually occur in cases when more intense responses towards slightly exaggerated stimuli are adaptive: preference for larger eggs, quicker response towards a potential mate, greater intake of calories. Therefore, the costs of overreacting to supernormal stimuli may be outweighed by the benefits, allowing for such responses to persist or even increase over evolutionary time. However, responses to such stimuli can also be exploited. For example, supernormal stimuli may enable brood parasites (species that use other species to raise their young ones) to take advantage of their hosts. If egg size or gape[1] size or colour are stimuli to which birds show parental responses (as described above), small host bird species might incubate eggs and rear chicks of brood parasites that are much larger than themselves (*Figure* 3). As Tinbergen wrote in 1965 [3], "....it is possible that many songbirds are not merely willing to feed a young cuckoo but simply love to feed it, just because the cuckoo offers such an enormous and inviting gape." It must be said here that the study of brood parasitism is a vast field and there are sev-

[1] The interior of the mouth that is often brightly coloured in young birds.

Figure 3. A Eurasian reed warbler feeding a common cuckoo (brood parasite) chick. Note the size difference between the foster parent and chick and the large, red gape of the chick. Photo by Per Harald Olsen. Source: https://commons.wikimedia.org/w/index.php?curid=1887345 under Creative Commons Attribution-Share Alike 3.0 Unported license (CC BY-SA 3.0), http://creativecommons.org/licenses/by-sa/3.0/deed.en.

eral hypotheses about why brood parasites exist. These include the 'mafia hypothesis', according to which, hosts that reject the brood parasite's eggs are punished by their nests being destroyed by the brood parasite [see 7], and the cost to the host of wrongly rejecting its own offspring when brood parasite eggs and chicks closely mimic those of its own. In the case of humans, positive responses to calorie-rich food, crucial in pre-agricultural societies faced with unpredictable access to food, is currently manipulated by the food industry through the marketing of supernormal (or 'hyperpalatable') foods. A wide range of other products are also marketed by the advertising industry tapping into supernormal responses.

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While supernormal stimuli may not be frequently present in an animal's environment ordinarily, a change in the environment may result in an 'evolutionary mismatch' [8] with responses that evolved under previous circumstances being out of sync with and possibly being maladaptive under the changed environment. For example, the evolutionary mismatch that humans face today, resulting in various supernormal responses being shown, possibly arise from the transition between the hunting-gathering lifestyle that we had for most of our lineage's existence and the relatively recent advent of agriculture. Responses do not have to be necessarily maladaptive in a new environment. If there are costs (say, in the form of predation) to displaying an exaggerated response to a supernormal stimulus, and if the environment changes such that the cost is removed, there may be selection for the supernormal stimulus (in the form of, say, brighter eggs or specific mate characteristics), thus allowing for divergence between populations and/or evolution of new forms.

Suggested Reading

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Address for Correspondence
T N C Vidya
Jawaharlal Nehru Centre for Advanced Scientific Research (JNCASR)
Jakkur
Bengaluru 560 064, India.
Email:
tncvidya@jncasr.ac.in
tncvidya@gmail.com