clusters, reducing it below the threshold for percolation.

Although some of the ideas in this paper have clear parallels with those in Turner's and Pitcher's [6] 'attack abatement' model, the notion of a critical *percolation threshold* triggering gregarious behaviour is entirely novel. The Reynolds *et al.* [2] paper is important for a number of other reasons. For one thing, this is the first time that percolation theory has been used to understand the benefits of group-living as an anti-predator defence. Indeed, although percolation theory is commonly used in physics, materials science, engineering and chemistry, less than 3% of the 1000+ papers published in this area over the last five years have addressed ecological or environmental issues (ISI Web of Knowledge).

Secondly, the paper illustrates how percolation theory might be applied more generally to understand the evolution of group-living [7]. Previous studies have argued that living in groups may have evolved as a defence against parasites and pathogens, because by aggregating together the connectivity between groups of potential hosts is reduced and there is an increased probability that disease epidemics sweeping through a population will fade out, because of a shortage of nearby susceptible hosts [8]. Whilst spatially-explicit agent-based models seem to confirm the benefits of group-living as an anti-parasite defence, percolation theory has not yet been applied in this context (but see [9]). However, it seems likely that percolation theory may provide a general theoretical framework for understanding the evolution of gregarious behaviour as a defence against any natural enemy that exploits clusters of hosts.

Thirdly, this study is important because it suggests that aggregative behaviour may have been the first step in the evolution of the suite of traits we commonly refer to as phase polyphenism. This is because it argues that there are benefits to individuals of congregating in groups even in the absence of any benefits associated with unpalatability, aposematic coloration or kin-selection. Once gregarious behaviour has evolved, selection would then favour other traits to maximise the benefits of group living and to minimise its costs, including the evolution of aposematism [10], cannibalism [11], and density-dependent prophylaxis [12]. Whilst a spatially-explicit evolutionary model has yet to be developed to explore these ideas fully, it seems likely that the use of percolation theory to study the evolution of aggregative behaviour will prove to be a highly significant advance. Hopefully, percolation theory will permeate further into mainstream evolutionary ecology than it has done since its origins more than a quarter of a century ago.

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# Perceptual Learning: Inverting the Size–Weight Illusion

**When one lifts two objects of equal weight and appearance but different size, the smaller object usually feels heavier. New results show that this size–weight illusion can be inverted after extensive training with objects in which the natural size–weight relationship is artificially reversed.**

**Marc O. Ernst**

The size–weight illusion, whereby a smaller object feels heavier than a larger one of equal weight, was first described over 100 years ago by Charpentier ([1]; see [2]). In the natural environment, an object's weight is positively correlated with its size. Thus when one lifts the larger of two objects, it is expected to be heavier. According to most hypotheses, the size–weight illusion occurs when this expectation is not met. In particular, it has been argued that the illusion might be caused by a mismatch between the sensorimotor prediction and the actual weight. According to this mismatch hypothesis, the wrong prediction would lead to motor commands scaled inappropriately for the object's weight. A few years ago, Flanagan *et al.* [3] disproved this hypothesis by showing that, after repeated lifting of the same objects, the sensorimotor prediction adjusts such that the load-force when grasping the objects is scaled correctly, while the size–weight illusion persisted. If not a sensorimotor mismatch, perhaps a perceptual mismatch causes the illusion, or is the illusion even independent of prior expectations?

In a recent paper in *Current Biology,* Flanagan *et al.* [4] report that the size–weight illusion can be inverted after extensive training with objects in which the size–weight relationship is artificially reversed. They also show that the load-forces adapt to this inverted relationship, and interestingly they do so much more quickly than the size–weight illusion. Because the illusion can persist whether or not the motor commands for lifting the objects are scaled correctly and because the illusion is adaptable, the authors conclude that the size–weight illusion is a purely perceptual illusion, caused by an unmatched prior expectation that comes from the statistics of the environment.

Why does the illusion adapt at a different rate from other weight judgements? Flanagan *et al.* [4] argue that the tasks of picking up an object and comparing weights, as during the illusion, involve different forms of knowledge: picking up the object involves knowledge about the weight of each individual object, whereas the knowledge involved in the size–weight illusion concerns the size–weight relationship of the entire family of objects. Given this argument, there should be no or little generalization of learning for the load-force parameter, because this is based on the identity of the individual objects (a steep generalization gradient), whereas there should be extensive generalization of learning with the size-weight illusion: it should generalize to the entire family of objects (shallow generalization gradient). Flanagan *et al.* [4] found some generalization in both cases. Unfortunately, however, they tested generalization of learning only for one new object, so it is unclear whether the generalization gradients actually differ.

At first glance, the finding of different adaptation rates for load-force and the size–weight illusion might seem like an example of a perception–action dissociation (for example [5–7]). According to this dissociation hypothesis, there are two visual systems: one for perception and one for guiding actions [8]. Load-force is indeed an action parameter and the size–weight illusion is seemingly perceptual [3,4]. But load-force, being based on knowledge about the individual object, and the illusion, being based on knowledge about the size–weight relationship of the entire family of objects, are also different in many other respects. Thus, it may be inappropriate to generalize from just these two parameters to a dissociation of perception and action on the whole.

Such a generalization, however, has already been suggested [7]. But this is even more questionable, as one could easily find other perceptual tasks involving weight estimates that adapt at different rates from the size–weight illusion. For example, in the work of Flanagan *et al.* [4], the participants very quickly became consciously aware of the fact that the small objects were very heavy and the large objects were very light. That is, after just a few lifts, participants could tell that the small objects were really heavy and the large objects were really light (Randy Flanagan, personal communication). Thus, if one were to measure the expected weight for the individual objects by simply asking the participants prior to lifting the object how heavy they think it will be, one can see that such a judgement adapts much more quickly than the size–weight illusion. Such a judgement is without doubt cognitive/perceptual and does not involve a motor response, which is why any general conclusion from just the load-force and the size–weight illusion about action versus perception is an overgeneralization.

An interesting remaining question is, why knowledge about the weights of the individual objects should be acquired at a different rate than knowledge about the size–weight relationship of the entire family of objects? After all there are the same number of objects involved in both learning tasks. In a recent study, Burge *et al.* [9] showed experimentally that the learning rate on the one hand depends on the quality of sensory information. On the other hand, the rate also depends on whether changes are to be expected or not (see also [10]). As Flanagan *et al.* [4] point out, individual objects are more likely to change in weight. Imagine, for example, a water bottle being more or less full, or a piece of wood that might be really light or quite heavy. Thus, adjustments in the load-force during handling of objects are very likely to occur in many everyday situations. Compared to this, it is very unlikely that within an object class the size–weight relationship is altered significantly. As Burge *et al.* [9] showed, one can describe the effect of the likelihood of change (process noise) on the adaptation rate quantitatively using a Kalman-Filter approach, which can be derived using the Bayesian framework.

It has been shown that many perceptual illusions can be described using the Bayesian framework [11]. By adapting the size–weight illusion after artificially altering the size–weight relationship demonstrates unequivocally that indeed the cause of the size–weight illusion is a comparison of the sensed weight with the expected weight given the size of the object. Thus prior knowledge is used that comes from the statistics of the environment. Using such prior knowledge representing the environmental statistics is a characteristic of the Bayesian approach (for example [12–16]). In the Bayesian approach, however, prior knowledge is integrated with the sensory evidence, which would produce an intermediate result weighting prior expectancy and sensory evidence according to their relative reliabilities [17]. In contrast, the size–weight illusion is a contrast effect and not average: smaller objects seem to be heavier. Thus the size–weight illusion is still a puzzling effect and it can even be argued that it is an anti-Bayesian effect.

In conclusion, despite over 100 years of research in which the size–weight illusion has been well described and characterized, we still lack a good explanation of why the illusion occurs — saying it occurs because the expectation is not matched and thus we perceive a contrast is only a description of the effect, and not an explanation.

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# Protein Complexes: The Evolution of Symmetry

**Most proteins form symmetric, multimeric complexes. Modeling shows that a strong prevalence for symmetry among stable structures can account for this bias even in the absence of other adaptive advantages.**

**Kevin W. Plaxco and Michael Gross**

Proteins like to stick together, especially with their own kind. While tallies vary it appears that for at least two-thirds of all proteins the preferred form is that of a complex (an oligomer) of several protein molecules (monomers) [1]. And while many of these oligomers are heterogenous — composed of more than one type of polypeptide chain — the majority are homogeneous, or are mixtures of the two (for example, hemoglobin is a tetramer made up of two identical copies of a heterodimer). Considering that protein molecules are asymmetric by default — as all but one of their building blocks are chiral — and their overall shapes are also highly irregular, it is surprising that the very large majority of these homogeneous oligomers form rotationally symmetric structures, ranging from simple head-to-head (as opposed to asymmetric head-to-tail) dimers to the beautiful 64-subunit icosahedral structures of many viral capsids. A recent paper by Baker and co-workers [2] sheds new light on the origins of the remarkable ubiquity of such symmetry.

Symmetry arises when two subunits interact via a symmetric interface in which amino acids x and y on one subunit interact with, respectively, their pendants $y'$ and $x'$ on the second subunit. But because protein surfaces are typically large and convex the simultaneous formation of such symmetry-related interactions is often hindered by geometry, and only a tiny fraction of all possible sets of homodimers will be symmetric. Given the discrepancy between the rarity of symmetric interactions among the set of all possible dimers, and the frequency with which symmetry occurs within the set of observed dimers, it has long been assumed that symmetry itself must provide a selective advantage. For example, it has been argued that rotationally symmetric structures are common because their formation saturates all of the available binding sites (which, for example, head-to-tail dimers fail to do), leading to closed structures of well-defined stoichiometry [3].

Baker and co-workers [2] advance an alternative theory: that symmetric structures are common because symmetric interfaces are over-represented among the set of all energetically favorable interactions. In other words, symmetric structures are common, not because they provide a selective advantage *per se*, but because stable, symmetric dimers are much more common than stable, asymmetric dimers in the underlying 'chemical space' of energetically favorable dimeric structures, and thus the former represent a larger, more accessible evolutionary target.

One of the oldest notions in probability theory, and the basis for statistical mechanics, is the observation that the more often one gambles the closer the average outcome of one's bets hews to the theoretical mean. Conversely, in the gambler's paradox, a punter who bets half as often but twice as much would double the variance of his expected outcome and thus flirts with ruin. The same principle also applies to the pair-wise energetics and evolution of proteins. For example, Monod, Wyman, and Changeux [3] noted that each interaction formed in the interface of a symmetric dimer occurs *twice.* Hence the impact of a favorable (or unfavorable) mutation is doubled for symmetric interfaces, increasing the rate with which evolution can optimize a symmetric structure once it is initially found. Baker and co-workers [2], however, have modeled Monod's conjecture using explicit protein-docking simulations and found that, while the effect is present, a counter effect works against it: because it contains only half as many unique amino acids, the mutation rate for a symmetric interface slows by a factor of two, limiting the impact of this mechanism. Instead they find that the gambler's paradox favors symmetric dimers by increasing the ease with which they are discovered in the first place.

Lukatsky *et al.* [4] recently studied identical interactions randomly scattered on two planar disks and found that the lowest energies of co-axially docked disks occur when the patterns on the opposing disks are the same rather than different (homodimers rather than heterodimers). They did not determine, however, how the density of states varies as the interactions deviate from symmetry, and thus the importance of their effect in the evolution of symmetry