Noise and Function

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Abstract

Noise is widely understood to be something that interferes with a signal or process. Thus, it is generally thought to be destructive, obscuring signals and interfering with function. However, early in the 20th century, mechanical engineers found that mechanisms inducing additional vibration in mechanical systems could prevent sticking and hysteresis. This so-called “dither” noise was later introduced in an entirely different context at the advent of digital information transmission and recording in the early 1960s. Ironically, the addition of noise allows one to preserve information that would otherwise be lost when the signal or image is digitized. As we shall see, the benefits of added noise in these contexts are closely related to the phenomenon which has come to be known as stochastic resonance, the original version of which appealed to noise to explain how small periodic fluctuations in the eccentricity of the earth’s orbit might be amplified in such a way as to bring about the observed periodic transitions in climate from ice age to temperate age and back. These noise-induced transitions have since been invoked to explain a wide array of biological phenomena, including the foraging and tracking behavior of ants. Many biological phenomena, from foraging to gene expression, are noisy, involving an element of randomness. In this paper, we illustrate the general principles behind dithering and stochastic resonance using examples from image processing, and then show how the constructive use of noise can carry over to systems found in nature.

1 Introduction

We are surrounded by noise. The controlled explosions of internal combustion engines combine with the roar of rubber on asphalt to create the drone of road and highway traffic. Weed-whackers, lawnmowers, and leaf blowers can turn sunny suburban summer days into a buzzing confusion. Indeed, the entire universe is filled with the faint din that is the cosmic microwave background (CMB) radiation, leftover electromagnetic radiation from the The CMB was discovered when Penzias and Wilson (1965) went looking for the source of annoying hiss plaguing their new radio telescope, hiss that threatened to obscure signals from distant stars and galaxies. Noise seems to be entirely destructive, thus something to be eliminated if possible.

Noise can be beneficial, however, in at least two ways. One is familiar, the other paradoxical and far less well known. The familiar way is simply as a source of variety. For example, genes undergo random mutation from processes both external to the organism (e.g. cosmic rays) and internal (Dobrindt and Hacker, 2001). This genotypic variation is the source of

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heritable variation in phenotype, which is of course essential for the process of natural selection (Wagner, 2014). Phenotype can even vary within isogenic populations due to variation in gene expression (Fraser and Kaern, 2009). This phenotypic noise is thought to provide an evolutionary advantage for some microorganisms, as it increases the chance that some will survive under stressful conditions. The CMB noise, though destructive from the standpoint of the users of radio telescopes, plays a constructive role in generating the tiny variations in energy density in the early universe that are the seeds of structure formation. The random fluctuations we call noise give rise to stars and galaxies and galactic clusters. This much is familiar, at least to those working in the relevant areas of biology or astrophysics.

Considerably less familiar is the role that noise can play in nonlinear systems, in particular systems with one or more thresholds, points at which small differences in input give rise to disproportionate differences in output. Converting an analog signal into a digital signal involves sampling the signal at regular intervals and writing down a digital approximation of the amplitude at each point. For example, if one has a one-bit digital system with two possible values to represent the interval from 0 to 1, then there will be a threshold at the analog value 0.5, below which any value will be digitally recorded as 0, and above which any value will be recorded as 1. More bits simply mean more thresholds, more ways to cut up the interval into discrete chunks. Neurons behave like single threshold devices, firing when and only when the voltage across the cell membrane reaches a certain activation threshold. What noise can do in a threshold system is push the signal over the threshold, but in a way very much unlike an amplifier. Amplifiers multiply the signal, whereas noise is additive. The implications and applications of this nonstandard amplification are both deep and wide. Here we will lay out as simply as possible the principles behind this sort of noise benefit and then illustrate its application.

2 Shades of gray: Noise in image processing

Photographs are never veridical. The information coming through the lens is inevitably greater than the information stored on the recording medium. A digital camera sensor has a finite spatial resolution; the camera’s sensor consists of a matrix of smaller individual sensors corresponding to a single “pixel” of the image. Any features of the image smaller than an individual pixel will be lost. Associated with each pixel is a color. The color spectrum in the real world is continuous, but the digital encoding of color is discrete, so that in general, the color stored will only be an approximation of the actual color. In other words, color information must be rounded off in order to be stored as a number on a digital computer. The number of binary places available for each number is referred to as the bit depth.

Suppose we have a digital image consisting of 7 megapixels. Let’s consider a “black and white” camera for simplicity, so that the colors are shades of gray. Each pixel has an 8 bit number attached to it indicating the shade of gray, with 0 (00000000) corresponding (by convention) to black, and 255 (11111111) corresponding to white. There are a total of $2^8 = 256$ shades of gray. Figure 1(a) shows the palette, alongside an image of a woman known as Lena (Hutchison, 2001), rendered using this palette (Figure 1(b)).

Now, suppose we want to print these images. Indeed, you may well be reading a printed version of this page, printed on a laser printer capable of printing 300 dots per inch (dpi). That resolution gives us around 7 million evenly spaced points on a typical sheet of paper, so if we were to use up an entire page to print the 7 megapixel image, we would have a one-
(a) 8 bit grayscale palette (256 shades)
(b) 8 bit Lena (256 shades)
(c) 1 bit grayscale (2 shades)
(d) 1 bit Lena (2 shades)
(e) 3 bit grayscale (8 shades)
(f) 3 bit Lena (8 shades)

Figure 1: Shades of gray
to-one correspondence between pixels and dots. If the printer could print 256 shades of gray at any given point, then we’d have perfect reproduction of the stored image. But the printer is not nearly that flexible. At each dot location, most printers can print either a black dot or nothing. Because the number of pixels and the number of dots are approximately the same (in our example), we are effectively reducing an 8-bit (per pixel) image to a 1-bit (per dot) image: 256 shades of gray at each point get mapped to either black or white.

The obvious way to map the shades of gray is to impose a threshold as before, whereby we print a black dot at a point if the corresponding pixel is more than 50% gray (numbers between 0 and 127), and we otherwise leave it blank (white) (numbers between 128 and 255). For an image that has an equal distribution of lighter and darker grays, this might appear to be as good as one can do. But a quick glance at Figures 1(c) and 1(d) shows the limitations of this simple thresholding method; an enormous amount of detail is lost. Increasing the number of thresholds to create 8 shades of gray, as in Figures 1(e) and 1(f), yields a noticeable improvement, but a printer that can only print in black and white is limited to the performance of the 2 shade case.

However, there are clever methods to improve the fidelity of black-and-white image reproductions. Traditional printed newspapers used varying dot size to represent darker and lighter portions of an image. Applying this halftone concept to a device like a laser printer or an LCD display with fixed dot or pixel size involves representing gray by varying the density of the distribution of black dots in an array. Using $3 \times 3$ arrays of dots, we can represent ten different shades of gray shown in Figure 2(a), which allows for a grayscale palette like that shown in Figure 2(b). A 300 dpi (dots per inch) printer can print $100 \times 100$ patches of gray per inch, where each patch has a $3 \times 3$ pixel area. Thus, with a three-fold reduction in the effective spatial resolution of the image, the number of shades which can be represented is increased from two shades to ten. The same technique could be applied to $4 \times 4$ arrays of dots to achieve seventeen shades of gray at the cost of further decreasing the spatial resolution.
Although deterministic methods like halftoning can be effective ways of trading spatial resolution for color resolution, they introduce noticeable artifacts. Note the abruptness of the shifts in the halftone grayscale palette in Figure 2(b). To avoid this blockiness while still being able to trade spatial resolution for color resolution, a very different approach can be used based on the appropriate addition of random variation to pixel values. For each pixel, we take the original grayscale value and add a random number between 0 and 255. An image made up of these random values would look like visual “noise” – it is a distribution of dots in arbitrary shades of gray. The result of adding this noise to the image is an array of pixels with values between 0 and 510. We can turn the resulting array back into an image by dividing the values by two, thereby restoring the original range of 0 (black) to 255 (white). Figures 3(a) and 3(b) show the result: noisy versions of the original grayscale palette and the original image. This of course is not an improvement over the non-noisy 8-bit grayscale image with 256 shades of gray. The noise does what we generally expect noise to do: it degrades the image.

But recall that we added the noise not to improve the grayscale image but to get a better result when we subsequently impose a threshold at 127 and convert to a black and white (2 shade) image. Imposing the threshold, we map any pixel with value 128 to white (255), and any pixel 127 or below to black (0). The resulting pseudo-grayscale palette that looks like Figure 3(c), while the resulting pseudo-grayscale Lena looks like Figure 3(d). The results are instructive. The grayscale palette looks better than the version in which noise was not imposed before thresholding (Figure 1(c)), giving the impression of a variety of shades of gray. Lena, however, does not look very good by comparison with Figure 1(d). The reason, as we noted above, is that given enough pixels, the ratio of black dots to white will closely approximate the degree of grayness of the original shade from the 256-color palette. For a large number of pixels, observed at a sufficiently great distance, we get an excellent representation of gray. The problem with the Lena image is not that she has more shades of gray, but that the shades tend to change over the scale of a few pixels. Images of this sort are better treated by more sophisticated techniques such as the Floyd–Steinberg error diffusion method (Floyd and Steinberg, 1976).

However, if we avail ourselves of 8 shades of gray (3 bits) rather than just black and white (1 bit), the use of random noise is much more effective. Figure 4(a) and Figure 4(b) show the original 256 shade images augmented with a low level of noise, spanning 1/8 of the total range (32 shades of gray). That is, the noise randomizes the 3 least significant bits (LSB) of the 8 bits in use. If we now reduce to to 8 shades (encodable by 3 bits) having added this noise, we get Figure 4(c) and Figure 4(d), which are a decided improvement on Figure 1(e) and Figure 1(f), which are what we get if we go from 256 shades to 8 shades without first adding noise.

The process of adding noise to an image or a signal in order to preserve information once the signal is subjected to quantization\(^1\) (digitization) is called dithering.\(^2\) In the example above, we took an already discrete signal (each pixel having one of 256 shades of gray) and made it more discrete, mapping the 256 shades into 2 shades (black and white). However, the initial process of moving from an image with a continuum of shades to one with 256 shades is also an example of quantization. Were we dealing with digital audio, we would

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1. “Quantization” here does not refer to the physicist’s process of finding a quantum-mechanical version of a classical theory, but rather the process of discretizing the properties of an image or signal.
2. Dithering also includes related methods that use, not random noise, but some other signal which is uncorrelated with the signal of interest. The ring laser gyroscope, for example, uses periodic (sinusoidal) dither to prevent its counter-rotating laser beams from locking under conditions of slow rotation.
Figure 3: Reduction from 256 shades (8 bits) to 2 shades (1 bit) using 8 bit random dither noise.
Figure 4: Reduction from 256 shades (8 bits) to 8 shades (3 bits) using 3 bit random dither noise (randomizing the 3 least significant bits (LSB)).
be working with a one-dimensional stream of samples of the waveform, each of which has
a continuously valued amplitude (the volume) that must be mapped into a finite set of
numbers for storage in a computer, say 24 bits (16,777,216 possible values). This can then
be further reduced to 16 bits (64,436 possible values) for CD encoding. Dither is routinely
used in this process.

Most digital representations involve more than one threshold. The seminal work of
Roberts (1962) considered the problem of transmitting digital television. At the time, a
6-bit-per-pixel resolution was considered adequate. Roberts proposed a scheme whereby a 3-
bit-per-pixel signal could effectively encode the necessary detail if pseudo-random noise were
added to the 6-bit representation prior to rounding to 3 bits.\(^3\) Shortly thereafter, others
realized that this technique was akin to a technique called “dither” that had been conceived
several decades prior as a technique to overcome the tendency of certain mechanical systems
to stick for various reasons, rendering them insensitive to small changes in operational
parameters (Schuchman, 1964). Engineers designed electromotor circuits to apply dither in
the form of small zero-mean oscillations that would allow devices to respond more easily
to small steering signals from the operator (Farmer, 1944; Korn and Korn, 1952). In all of
these cases, proper application of dither tends to linearize a nonlinear system; the dither
blurs thresholds, eliminating some of the jaggedness that goes along with systems that have
one or more thresholds.

But the addition of noise does something else along the way. In a physical system, adding
noise adds energy to the system. If the system has one or more thresholds, this has the
effect of taking subthreshold signals and boosting them, albeit stochastically. This is the
phenomenon known as stochastic resonance. Let’s take a look at a simple example, again
using printed images, before moving on to the role stochastic resonance can play in natural –
including biological – phenomena.

We’re accustomed to the fact that there are sounds we can’t hear because they’re too
soft, and sights we can’t see because they’re too faint. These are thresholds of hearing and
vision, respectively. By analogy, consider an image we can’t make out because it’s too light:
a very light shade of gray indistinguishable from its white background. Figure 5(a) shows
the full grayscale palette with a line separating the grays that are dark enough to distinguish
from those that, for some focal individual, are not. We can represent the indistinguishability
of any grays below the threshold by rendering them as white, as in Figure 5(b). Thus, when
a faint image of the words ‘Phantom Engineer’ (Figure 5(c)) is rendered in this very light
gray, it will look like Figure 5(d) to someone for whom this threshold represents the limits
of their perceptual acuity. The image will be invisible.

Now, suppose we add noise by randomly darkening each pixel, including the background.
We will use low-level, 3 bit noise, as shown to the right of the vertical bar in the grayscale
palette depicted in Figure 6(a). This corresponds to randomly selected shades of the very
light grays lying below the threshold of perceivability. Thus, like the image itself, the noise
will be invisible – see Figure 6(b) – to someone who cannot make out very light shades of
gray. Adding this noise to our original image as in Figure 6(c) has the remarkable effect of
bringing a noisy but very legible version of the image above the threshold of perceivability,
as is evident in Figure 6(d), in which the lightest, sub-threshold grays are removed. The
ability of noise to boost a signal above threshold is the essence of stochastic resonance.

One of the salient characteristics of stochastic resonance, indeed the feature that makes
it somewhat akin to a true resonance phenomenon, is the dependence on the amplitude and
\(^3\)The scheme of Roberts (1962) was an early example of what is called subtractive dither, where the noise
is subtracted from the image after transmission
Figure 5: Rendering a signal imperceivable by thresholding. The signal is too light to survive the imposition of the threshold.
Figure 6: Stochastic resonance: signal boosting with noise. Random dither noise spanning the 3 least significant bits (LSB) is added. With the addition of noise, the signal becomes dark enough to remain visible even after the imposition of the threshold.
specific properties of the noise. This is true of either noise in general. Too much noise (here, too large a spectrum of grays) threatens to obliterate the signal, while too little will fail to push the signal above threshold at all, and have no effect. The relevance of this for understanding the role of stochastic resonance in nature is significant, for there is noise of all kinds and all amplitudes everywhere. Oftentimes it does what we think noise does: it interferes with the signal, the image, or the operation of a dynamical system. But when the noise level is proportional to the level of one or more significant thresholds in a system of interest, we can and should look for stochastic resonance, as it may be key to understanding the function of the system (Gammaitoni et al., 1998).

3 Amplification by noise in natural dynamical systems

We will now take a look at how the stochastic resonance effect can be used in modeling a dynamical system existing in nature. The example we’ll study is the one in which the term ‘stochastic resonance’ was originally introduced. Though there is no resonance in the ordinary physicists’ sense (though see Gammaitoni et al., 1995), we are once again presented with a situation in which the addition of noise permits the system of interest – in this case the climate – to straddle a threshold.

The earth has existed in two relatively stable climates around 10 degrees Kelvin apart for millions of years. Periods in which the climate is cooler are called ice ages. In the late 1970s (Bhattacharya and Ghil, 1978), it was conjectured that the two stable climates correspond to the two-minima of a double-well pseudo-potential like the one shown in Figure 7. The horizontal axis represents the earth’s temperature, and the curve acts like a potential energy term in ordinary mechanics, with a single unstable equilibrium forming an energy barrier between two stable equilibria. In this model, the earth’s climate inevitably converges to one of the two stable equilibria. The equilibrium on the left represents the ice age, and the one on the right is a temperate period like the present.

Thus, we have a primitive model of a system with two stable states. But the stability of these states means that there is no way to transition between them, thus no way to explain how the climate shifts from one to the other. However, it was observed that the eccentricity of the earth’s orbit varies over a period roughly the same as the time between ice ages – around 100,000 years (Hays et al., 1976). Because the eccentricity of the orbit is correlated with small variations in the amount of solar heating (“insolation”), it was conjectured that these small variations might be sufficient external drivers of the earth’s dynamical system to cause the observed periodic climate changes. This suggests that one augment the model by introducing a time-varying oscillation in the pseudo-potential in which the double-well shape is a transient feature separating two epochs in which the potential morphs into a single well, a single quasi-stable equilibrium.

The problem with this idea was that the estimated insolation differences were too small to be responsible for such a change. At best, the resulting time-varying pseudopotential takes forms like those in Figure 8, where the barrier between the two stable equilibria is always maintained, and where the change in temperature due to the displacement of each local minimum is of the order of only 1 degree Kelvin. So a simple dynamical systems approach does not provide an explanation for the congruence of the period of the insolation signal and the period of earth’s climate switching.

Independently, Nicolis (1982) and Benzi et al. (1982) arrived at similar explanations for how the climate might actually shift. They proposed that including the fine-scale, shorte-
time variations in heating and cooling due to various other factors might result in the climate hopping from one well to the other. In other words, factoring in the existence of a certain level of noise in the climate system might account for the ability, as it were, of the climate to surmount the otherwise insurmountable threshold, the hump between the two minima. After all, the geological record shows not only periodicity in the earth’s climate but also significant small-scale variations which indicated that the earth’s dynamics must include some internal noise. So, following the approach of Nicolis, the deterministic double-well pseudo-potential is augmented with a noise source, converting an ordinary differential equation into a stochastic differential equation. In other words, the climate is now modeled as a diffusion process – a random walk that is pulled downhill but can, on occasion, take several steps uphill. For such a diffusion process in a double-well, the mean time to transition from one stable equilibrium to another is well characterized by a formula parameterized by the height of the barrier between the equilibria and the strength of the internal noise. What Nicolis realized was that the changes in the barrier height due to noise could lead to large changes in the mean residence time. If the noise is of the right amplitude, then the climate is likely to hop from one not-quite-stable minimum to the other when the barrier is low. Consequently, Benzi et al. (1982) named the phenomenon stochastic resonance based on its similarity to the frequency-selective properties of conventional deterministic resonance. Whereas “resonance” in the traditional sense is between the frequency of an input and the characteristic response of a system, the resonance here is between the frequency of the long-term oscillation in insolation (the input) and the amplitude of the noise (a characteristic feature of the system). If the noise is too small, nothing special will happen; the system will
Figure 8: Time-varying double-well pseudo-potential with period of 100,000 years
never transit from one climate to the other. If the noise is too great, the system will never settle in one climate or another, as the noise will dominate the oscillation. If the noise is within the correct range, however, the climate will oscillate at approximately the 100,000 year period of the subthreshold background oscillation in the ellipticity of the earth’s orbit.

4 Noise in living systems: decision making in ant colonies

Over the past 20 years, an intriguing body of evidence has pointed to a role for stochastic resonance in a variety of biological processes (McDonnell and Abbott, 2009). Extensive work has been done demonstrating the role of noise in general and stochastic resonance in particular in the neural systems that carry out sensory information processing (Moss et al., 2004), but it is important at the macroscopic level as well. We will conclude our discussion of stochastic resonance by discussing its role in the social dynamics of group decision making in certain species of ants.

There are a wide variety of mass-recruiting ants that form charismatic foraging trails that concentrate all foraging effort onto a single food source for a short period of time (Hölldobler and Wilson, 1990). As many species of mass-recruiting ant have a heterogeneous foraging force, it is thought that it may be beneficial to concentrate the foraging force all in one area in order to guarantee there is an adequate representation of each worker type. So it is expected that these ants must make use of some decentralized mechanism that can drive its foraging force to a quick consensus on the best of several available foraging options.

A typical feature of mass-recruiting ants is the use of pheromone trails (Hölldobler and Wilson, 1990). Although details vary across different mass-recruiting ant taxa, the observed pattern is usually a variation of what follows. A focal ant leaves her nest and searches for food. When she finds food, she can choose to return to her nest and deposit some quantity of pheromone along her path back to the nest. The amount of pheromone she deposits is related to the quality of the discovered food, with higher-quality foods leading to more deposited pheromone. Although that deposited pheromone will eventually evaporate, for a short time after deposition, the pheromone near the nest will attract the attention of other foragers that would otherwise search randomly for food. They will then have an increased likelihood of finding the same food source as the focal ant and then also lay a pheromone trail on their return visit. So initially, a set of food items will be discovered randomly. Due to the positive feedback inherent in the recruitment system, the highest quality of those food sources will eventually attract all of the foragers.

Until recently, it has been believed that such trail-laying mass-recruitment mechanisms had a flaw similar to the one described in Section 3 for the early deterministic models of climate change – the ants were thought to be rigidly bistable and unable to cope with changes in food availability after a critical point in the recruitment process. In other words, the positive feedback in the recruitment would eventually become so strong that the system would become entirely insensitive to changes in relative food-source quality, just as early mathematical models of climate change were not properly sensitive to the variations in insolation. This intuition was verified in early experiments with *Lasius niger* (Beckers et al., 1990). Moreover, early dynamical mathematical models of trail-laying were also shown to be insensitive to changes in relative food quality (Camazine et al., 2001; Nicolis and Deneubourg, 1999). However, several recent experiments show that many other trail-laying ants are able to dynamically re-allocate their foraging forces to track changes in the environment (Dussutour et al., 2009; Latty and Beckman, 2013; Reid et al., 2011). For example, Dussutour et al.
Figure 9: Graphical summary of dynamic foraging experiment used by Dussutour et al. (2009) to study flexibility of trail-laying in *Pheidole megacephala* big-headed ant colonies. In the first 60 minutes of the experiment, colonies are given a choice between two feeders, A and B, that only differ in distance to the nest. During the second 60 minutes of the experiment, the nearest feeder (A) is removed. Finally, during the final 60 minutes of the experiment, the nearest feeder (A) is replaced.

Dussutour et al. (2009) presented colonies of *Pheidole megacephala* with a laboratory dynamic environment summarized in Figure 9. During the 180-minute experiment, colonies were placed at the mouth of a Y-bridge with two legs of different lengths, and the experiment proceeded in three 60-minute phases:

- During the first 60 minutes, equal-quality feeders were placed at the ends of both legs. Because one leg was shorter, it eventually dominated the collective attention of the colony and a single trail was formed to the feeder on that leg.

- During the second 60 minutes of the experiment, the feeder on the short leg was removed. With the disappearance of food, the pheromone trail was not reinforced, and the colony was eventually able to return to random search and subsequently converge on the feeder at the end of the long leg.

- During the final 60 minutes of the experiment, a feeder was returned to the short leg of the Y-maze. The traditional model of trail-laying recruitment would predict that the new feeder would be ignored because all foragers would be latched into following the existing pheromone trail. However, contrary to those predictions, the short leg was re-discovered and ants returned to exploiting the closer feeder.

To explain the results of the experiment, Dussutour et al. propose a slight extension to the traditional mathematical model of trail-laying recruitment inspired by stochastic resonance. They observed that ants in their experiments would often make “errors” in their trail-following behavior that would lead a minority of the ants down the opposite leg of the Y-maze. In an attempt to capture this phenomenon, they augmented the traditional mathematical model of trail-laying behavior with an “error” level that would cause an individual to rarely, but measurably often, choose the leg of the Y-maze with the smaller quantity of pheromone deposited on it. At small error levels, the theoretical system had
nearly identical decision-making latency and accuracy characteristics to the deterministic system when presented with a static choice set. However, at specific non-zero error levels, the system could produce switching dynamics that matched those of experimental data from ants like *P. megacephala* that have the ability to follow changes in relative feeder quality. Furthermore, the mathematical model predicted that different error levels would correspond to different random natural switching times between alternatives, and amplification of variations in food quality would be possible if the periodicity of those variations matched the natural error-driven switching time.

The time-scale matching argument for the switching behavior observed in some trail-laying, mass-recruiting ants is identical to the one used in the early models of stochastic resonance in climate systems that are matched to the periodicity of solar insolation. However, in the case of the ants, differences in error level across different ant taxa could be explained by natural selection. In particular, the individual error level could be tuned by natural selection so that the stochastic switching time of the colony would match the natural periodicity of changes in food quality in the natural environment. Colonies with individuals that make errors at the appropriate rate would have an advantage over colonies that make more or fewer errors. Making too many individual-level errors would mean switching too frequently from good choices to bad choices, and making too few individual-level errors would mean focusing for too long on one choice even though a better choice was now available. Consequently, the “errors” at the individual level would be better described as random variability (noise) that was itself a trait under selection, and the prediction would be that ants evolved in more ephemeral environments would also have larger amounts of noise in individual-level response to pheromone trails. In fact, as Dussutour et al. (2009) discuss, the flexible *P. megacephala* ants in their study that are well modeled by non-zero noise do come from an environment where food quality changes more frequently than the *L. niger* ants that had previously been used to support the deterministic modeling of trail-following behavior with no noise. If location of the best-quality food source is viewed as a signal that tends to change over some characteristic time scale, then the current location of the main foraging trail can be viewed as a version of that signal amplified using stochastic resonance. This argument is identical to those made in the stochastic-resonance literature where some input-to-output measure, such as mutual information, is maximized by varying the amount of noise added to the input signal (Neiman et al., 1996). Similarly, in the earlier image processing example, a certain amount of noise is sufficient to push the text ‘Phantom Engineer’ above the threshold of visibility (Figure 6). Too little noise will not do the trick. Adding noise will make the text more visible up to a point, after which the readability goes down as the entire image becomes dominated by noise. In the case of the ants, the signal being amplified is the relative quality of the feeders, and the output is the selection of a path by the colony.

The idea that apparent “errors” could actually be an adaptive phenotypic trait under selection is not unprecedented and goes beyond the examples of possible stochastic resonance in natural phenomena. For example, the idea that noise can be of benefit in decision making is relatively old. For example, in what they called “ethological cybernetics,” Haldane and Spurway (1954) performed an information-theoretic analysis of the statistical distributions of honeybees responding to communicated information from so-called “waggle dances.” Honeybees have the ability to communicate information from one forager to another through a dance language that communicates the relative polar coordinates (i.e., distance and direction) of a discovered food source. However, after a bee communicates these coordinates to another, the bee receiving the information will often make “mistakes” and explore a lo-
cation slightly different from the one discovered by the original bee. The average location explored by an ensemble of receiver bees will closely match the originally discovered food source, and so these variations are viewed as “noise” due to imperfect communication of the coordinates in the dance-communication channel. Haldane and Spurway determine that the bee-to-bee channel communicates roughly 4 bits of information about the direction of the target. That is, a bee can only communicate 1 of 16 different cardinal directions; any finer resolution appears to be impossible. This may seem to reflect a fundamental limitation, such as a physiological or neurological constraint, but it could also be an adaptive response to dispersed food sources in an environment. If a honeybee is dancing to communicate the location of a nectar source, such as a flower, the resulting noisy scatter of her colony mates will likely find other flowers in a similar location. Thus, the amount of error in the communication may be tied to some ecological measure of forage patchiness, and honeybees selected for environments with a different patchiness may communicate with different levels of error.

As the honeybee example does not involve dynamically changing signals in the environment, it is not an example of stochastic resonance in the strict sense, but it does reflect how the amount of noise expressed in a behavior is itself a phenotype that nature can adapt to match natural variation. However, a very similar information-theoretic analysis of fire ants does suggest additional ties to stochastic resonance and behaviors shaped by nature. In particular, Wilson (1962) described a consistent error distribution in the distance and direction information communicated by fire-ant pheromone trails leading to prey. In the trail-laying examples above, the actual food sources were static, and the experimenters could change the location of different sources at discrete instants of time. This was appropriate for the particular ant species under study. However, fire ants are a natural example of a species adapted to continuously varying food quality and location. These ants track moving food sources: living prey items that have the ability to flee. They must have the ability to dynamically adapt and follow fleeing prey until the prey is sufficiently subdued. Wilson suggests that the relatively poor ability of individual fire ants to follow trails is actually an adaptation. The result of the ensemble of error-prone trail followers is a cloud of ants in the general vicinity of the original location of the discovered prey. If this cloud is large enough, it can track the motion of the escaping prey. Too much noise will cast too large of a net and lead to too thin coverage over a prey item, and too little noise will not disperse the ants far enough to catch the escaping prey. So the dispersal of the trail followers could be matched to the escape dynamics of the typical kinds of prey. Just as in traditional stochastic resonance examples, a certain critical amount of noise helps a dynamic output (the ultimate location of the end of a fire-ant foraging trail) follow a dynamic input (the trajectory of an escaping prey item).

5 Conclusion

An ant colony’s ability to react to changes in the food supply and the climate’s ability to react to small changes in insolation are examples of the power of noise to qualitatively change the way a system responds to its environment. If we disregard the noise – disregard the small, random variations in the properties of the system – we find the system converges to a fixed point of its dynamical equations and stays there indefinitely. The ant colony remains fixated on a single food source, insensitive to changes in food supply; the climate remains where it is, never shifting. But when the model of the system is modified to include
noise, the system is able to surmount a barrier and transition to a qualitatively distinct state. The colony is able to discover and consolidate a new path. The climate reacts to the slight change in insolation over the course of millenia. Noise makes these systems more sensitive to their environment.

A promising area to look for further noise effects in biology lies at smaller scales. The fundamental process at the foundation of all life is the expression of genes as proteins. The chemical reactions involved are constrained by both the availability of the reactants and their proximity, making the process as a whole subject to fluctuations which have come to be called gene expression noise (Kærn et al., 2005). The sources of the noise and the role it plays in the process of development and reproduction are matters of intense contemporary investigation (Sanchez et al., 2013; Viney and Reece, 2013). For example, Fernando et al. (2009) proposed the existence of an intracellular genetic perceptron, a single cell gene network capable of associative learning. Remarkably, Bates et al. (2014) show that the performance of the perceptron is actually enhanced by gene expression noise at a specific level.

One of the factors impacting gene expression in bacteria is the intercellular communication mechanism broadly known as quorum sensing, in which bacteria both emit and detect signaling molecules, allowing them to infer the concentration of other bacteria and act accordingly (Popat et al., 2015; Waters and Bassler, 2005). This, too, is a noisy process, subject to the whims of diffusion in the intercellular environment. Like the examples of stochastic resonance we have considered, it is a threshold-oriented system, whereby genes are switched on or off depending on whether a critical density of other bacteria are sensed in the neighborhood. Karig et al. (2011) have applied stochastic resonance to the development of a synthetic biological system which utilizes gene expression noise to boost a time-varying molecular signal consisting of varying concentrations of the molecule used by Gram-negative bacteria in quorum sensing.

The recent, fascinating work on the role in biological systems of stochastic resonance in particular, and noise in general, is surely the tip of an iceberg. Hoffmann (2012) advances the idea that the molecular machines like kinesin that do physical work within the cell make use of the random noise that is the thermal motion of the water molecules in the cytoplasm. Rolls and Deco (2010) provide an extended look at the role of noise in brain function. The idea that noise can and does do work, enhancing the information processing that is essential to life, is an idea whose time has come.

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