Chapter 4

Harmonic Resonance in the Brain

We have seen that harmonic resonance exhibits some extraordinary and unique properties as a potential computational and representational mechanism even in a simple acoustical box, capable of generating reified spatiotemporal patterns that are causally coupled to a resonance mechanism that encodes those same patterns in an abstract symbolic code, using a Fourier type sinusoidal basis set. In Chapter 1 we saw that harmonic resonance is exploited by nature in embryological morphogenesis, as a spatial patterning mechanism for defining and reifying the spatial patterns of the body. But is harmonic resonance also exploited by nature as a computational and representational principle in the brain? In this chapter we will discuss the evidence for harmonic resonance in the brain, where it performs the same kind of function that it does in morphogenesis, and how it evolved from similar resonances in simple nervous systems, tracing back to resonances in some of the simplest creatures on the evolutionary scale.

Ascending the Evolutionary Ladder

The ultimate source of the electrochemical resonances in the brain and nervous system can be traced back to the properties of the animal cell. The earliest pre-cellular forms of life likely consisted of a loose confederation of chemical processes interacting in intricate feedback loops in rock pools or thermal vents. Eventually, a cell membrane evolved to prevent the vital components from simply drifting away into the primeval soup, to enclose the essential components in a semi-permeable bag, that self-assembles out of its component lipid molecules, which are manufactured by the molecular machinery of life for that purpose. The cell wall necessarily has to allow essential nutrients to permeate into, and waste products to permeate out of the cell, while containing the larger protein and genetic molecules essential for the biological machinery. But with the emergence of a cell wall, there immediately arose a problem, because the intra-cellular fluid has a high molarity due to all the heavy molecules of life that are dissolved in it, and thus osmosis creates a constant flow of water into the cell from the outside, that threatens to swell the cell and burst the plasma membrane. Bacteria and plants solve this problem by brute force, by making a polysaccharide cell wall that is tough enough to withstand the osmotic pressure, which can amount to tens of atmospheres, creating rigid cells with walls as tough as a pneumatic tire. Animal cells, in contrast, are in osmotic equilibrium with their environment and thus they

are much more soft and flexible, and can take on a variety of different shapes that can change from moment to moment, like an amoeba. In animals the osmotic balance is maintained by a trans-membrane protein molecule known as a *sodium pump*, that is constantly pumping sodium ions out of the cell, against a concentration gradient, which also draws water out of the cell, and this maintains a constant electrical voltage, or *membrane potential*, across the cell wall in the order of 60 -100 mv, negative inside the cell and positive outside it, like a charged capacitor. The energy required to pump the sodium ions against the electrochemical gradient, and this energy is provided by ATP, the fuel used in living cells. The sodium pump is just one of a number of trans-membrane proteins that automatically embed themselves in the cell wall, that can open or close like a valve, allowing a flow of ions into or out of the cell, but preventing the escape of large protein molecules from the cell.

Many animal cells are endowed with voltage-gated channels that will open for a brief period, whenever the membrane potential drops below some threshold voltage, allowing a free flow of positive ions back into the cell. Neurons and muscle cells possess greater concentrations of these voltage-gated channels in their cell walls. This has a destabilizing effect on the membrane potential, because a small drop of membrane potential at some local point in the membrane for any reason, will tend to spread, resulting in an abrupt and total collapse of the membrane potential across the whole cell, as more and more channels open along a spreading wave of depolarization. After a brief refractory period, the ion channels slam shut again, which allows the sodium pumps, which are running continuously, to instantly restore the membrane potential across the cell wall, which creates a wave of re-polarization as the cell returns to its normal electrical imbalance. If the conditions that triggered the first depolarization prevail, this can lead to a continuous burst of repeating depolarizations, or a train of spikes of a spiking neuron, or a continuous vibratory contraction, or tetanus, in muscle cells. Neurons (and many other cells) are also equipped with chemically gated channels, that open in response to some particular neurotransmitter molecule locking into place on them from the extra-cellular fluid, causing a local depolarization of the membrane at that point, and these chemically gated channels can provide the trigger that sets off the series of periodic depolarizations that constitute a spike train of the spiking neuron. Although the opening and closing of electrically gated channels is generally in synchrony with the spiking discharges that they trigger, studies of the micro-structure of the temporal pattern reveals a more complex picture. Patch clamp experiments that record the state of

single channels in an isolated patch of the plasma membrane have revealed a stochastic, or chaotic noisy pattern to the opening and closing of the channels on a time scale that is very much faster than the frequency of the typical spike train, (Sakmann & Neher, 1995) and some researchers have found stochastic resonance as a collective property of ion channel assemblies in somewhat larger patches of cell membrane. (Schmidt et al. 2001).

Although the opening and closing of electrically gated channels seems to be a random or chaotic process, it is possible that the process is not really random after all, but only appears so because we have not yet identified the causal agent behind it. It could be that this rapid opening and closing of voltage gated channels is not actually random or chaotic, but it could plausibly be in synchrony with a tiny voltage oscillation, or ripple voltage, superimposed on the larger voltage fluctuations of the action potentials when they arise, which in turn represents the electrochemical standing wave at that location in the neural tissue. That is, perhaps the electrical-gated channel serves the purpose of the diode in Figure 3.2 B, that opens during the positive phase of the oscillation and closes during the negative phase. In the presence of a noisy stimulus, like the sounds in many natural environments, it too would follow a generally random or chaotic pattern of positive and negative polarity. The apparently chaotic pattern of the opening and closing of individual ion channels is just a reflection of the complexity of the waveform of the electrochemical standing wave at that location in the neural tissue. In all but the most simple sensorimotor conditions (such as during an epileptic seizure, or tetanus), the waveform is a summation of many waves through a range of frequencies and phases that only appear chaotic at an isolated sample point. Whe viewed in the aggregate, as a spatial whole, even a complex chaotic waveform can be represented by a series of harmonics, as in a Fourier transform. It is the spatiotemporal patterns of those resonances that carry the significant sensory and motor signals, not isolated point samples of those signals, and the spatial wholes are also the aspect of neurophysiological activity of which we are consciously aware.

Perhaps the spiking neuron serves the purpose of energization and amplification of an analog waveform, like the reed of a wind instrument, whose vibratory motions are energized by a stream of air, but the vibration is a process is not confined to the reed alone, but involves the acoustics of the instrument as a whole. The purpose of the spiking neuron is not to register or record the pattern of electrical voltages received through its receptive field, as suggested by a feature

detection paradigm, but acts somewhat like an antenna that both recognizes, resonates to, and energizes a spatiotemporal standing wave in neural tissue.

The biochemistry of the animal cell at the level of ion channels and trans-membrane proteins is very much more complex and elaborate than is covered in this quick summary, with most channels specialized to channel only one type of ion into our out of the cell, some gated electrically, others chemically, in response to a staggering array of different specialized neurotransmitter substances that each act on only their own specific chemically gated channel, with either excitatory or inhibitory consequences. But whatever the complexity of the systems of chanels and their neurotransmitters, there is no question that the molecular machinery of a single cell has the capacity to generate electrical voltages across the cell membrane with its sodium pumps, and to release that voltage periodically in abrupt depolarizations with electrically gated channels. This is easily enough machinery for a harmonic resonance mechanism with the capability of establishing and maintaining self-sustaining electrochemical oscillations across the cell membrane. And indeed, many animal cells, not only neurons, exhibit all kinds of electrical oscillations in a great variety of frequencies and waveforms, as amplified vibrations powered by ATP. The animal cell fairly pulses with electrochemical energy in a process that consumes energy continuously. The brain hums continuously with what Pribram (1971) has called *graded potential oscillations* (analog voltage oscillations) even in the absence of the overt action potential of the spiking neuron. There is no shortage of plausible neurophysiological hardware available to the animal cell to account for a harmonic resonance even within a single isolated cell, once you understand the inherent computational and representational capacities of a harmonic resonance system.

The cilia of the paramecium reveal a coherent wave-like propagation of some kind of signal, most likely an electrochemical travelling wave, that synchronizes the waving of its innumerable cilia to a coherent motor plan. The synchronous waving of the cilia clearly indicate the presence of a harmonic resonance in the plasma membrane even at this tiny single-cellular scale. Other single-celled creatures use a flagellum for propulsion, a long whip-like tail like that of a spermatozoa, which is composed of bundles of long protein molecules called microtubules that shift, lengthwise against each other in synchrony to produce the contractions and extensions that travel down the length of the flagellum. The undulatory or spiral-rotary motion of this extraordinary molecular tail is also clearly some kind of travelling wave resonance, that synchronizes and coordinates the local

deflections at each point along the wiggling tail through local interactions with their immediate neighboring regions, to a globally coherent spiral or wavey pattern. Like the spermatozoa, many of these flagellated creatures exhibit goal-directed behavior, an ability to steer themselves toward some attractive stimulus, or away from some aversive stimulus. In the case of the spermatozoa, it is a chemical gradient that points the way toward a fertile egg. The Euglena, a single-celled flagellated animal capable of photosynthesis, is attracted toward light, whose direction it must somehow sense, and that sensory signal somehow modulates the pattern of waving of its flagellar tail. So even at this tiny microscopic scale we see creatures that close the full sensory-motor loop, whose motor system clearly involves travelling-wave resonances at a tiny single-cellular scale. Exactly how the sensory receptors of these tiny organisms control their flagella to steer towards the goal is not yet understood in any detail. But what is clear, is that whatever that sensory mechanism might be, it must have the effect of being able to intelligently modulate the patterns of resonances in the propulsive undulations of the tail, a sensory mechanism with causal effects on the oscillations of a resonance based propulsive mechanism.

In fact, this buisness of controlling sustained resonances has been the age-old pursuit of musical instrument makers for thousands of years, to devise resonating acoustical systems whose resonances can be modulated or controlled on demand. In the case of wind instruments, like the flute or clarinet, open holes damp the oscillation at that point in the tube, short-circuiting the oscillations of the vibration, triggering the formation of a node of oscillation at that point, whereas in string instruments the damping is achieved by pressing the sting against the fretboard with a finger.

Even at this microscopic single-cellular scale, the problem of sensory integration arises. A chemically guided organism presumably samples the chemistry of its external environment as does any other animal cell, that is with specialized trans-membrane proteins that have a special lock-and-key relation to the particular chemicals to which they respond, and the objective of the organism is to steer in the direction with the higher concentration of that attractor chemical. Many single-celled paramecium-like creatures exhibit this kind of chemotaxis. But if the sensory system of a single cell is composed of an array of trans-membrane proteins distributed somewhat randomly across its cell wall, how is the organism supposed to sense the pattern of those individual stimuli, to modulate the propulsive undulations of the multiple cilia, or a single tail, to steer the organism in

the required direction? How would that signal energize or modulate the wave-like propulsive undulations observed in cilia and flagellae? Harmonic resonance offers a plausible explanation for this phenomenon. Suppose that the waves of electrochemical energy that put the wiggle in the sperm's tail, begin not at the base of the tail, but pervade the cell body of the sperm cell, starting at the anterior pole opposite the base of the tail, as suggested in Figure Figure 4.1. A. Perhaps
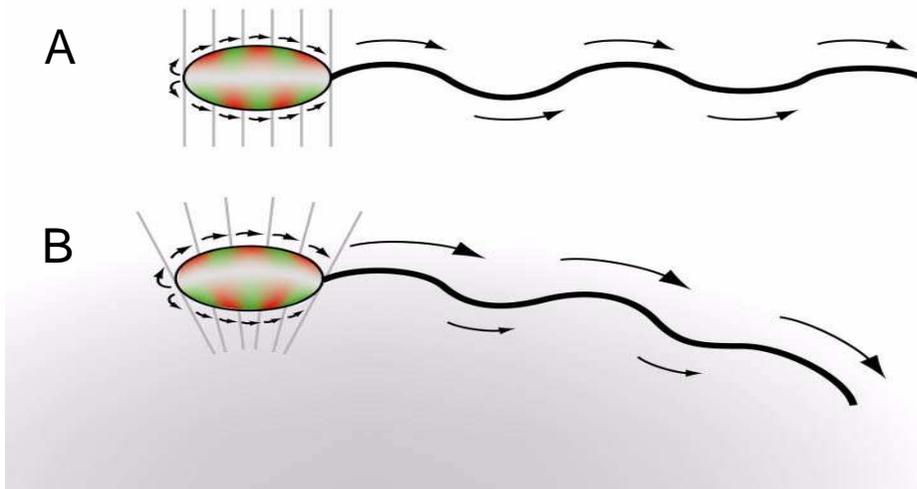

Figure 4.1. Wave model of sperm motor control, with A: waves triggered in the anterior pole of the cell body propagate to the posterior pole and beyond through the flagellum. B: The sensory system of the sperm has the effect of slowing the waves on the side of the organism closer to the stimulus, represented by gray shading, while speeding up the waves on the side away from the stimulus, resulting in a turning moment superimposed on the propulsive undulations.

the anterior pole is richly endowed with electrically gated channels, and thus tends to go off spontaneously, triggering waves that propagate down the cell body and continue down the tail. All that a sensory system would have to do is to find a way to modulate the phase of that wave, to slow it down on the side of the organism toward the stimulus, and speed it up on the opposite side, as suggested in Figure 4.1 B (or the reverse, for aversive stimuli). This would produce an asymmetry in the oscillations of the tail, steering the tiny organism in a curve. And all that would be required to modulate this travelling wave oscillation is a change in the dynamic parameters of the electrical oscillation across the membrane, something that might be easily accomplished by the opening or closing of chemically gated channels, which could either accelerate or delay the time required for electrical repolarization after each action potential. So the sensory integration of the individual ion channels as each one detects individual molecules of its target chemical in the extracellular environment, is achieved by summing or pooling the effect of each brief opening and closing of the chemically gated channel, as the individual gulps of ions released into the cell build up into pools of ionization inside

the cell. If the ionic imbalance across the cell dissipates rapidly as soon as the stimulus is removed, that gives the ionic gradient the ability to respond rapidly to changes in the chemical gradients in the extracellular medium. And if the resonance is self-amplified, then even the subtlest enviromnental gradient would tip the balance of the intracellular resonances, breaking the symmetry between the otherwise equal balance of harmonics in different directions, like the opening of holes in a flute that select between discrete resonance patterns that pervade the body of the flute. The significant feature of this chemosensory system is not so much its absolute concentration, as much as the *gradient* of concentration across the cell. This gradient is copied, or mimicked by a resulting electrical gradient across the cell membrane, whose asymmetrical application across different sides of the microorganism produce a corresponding warp, or asymmetry in the resulting propulsive undulations. It is a spatial representation, expressed as a diffusion gradient across a volume of intracellular plasma, that controls a spatially reified spatiotemporal pattern of motor control. The computational problem of sensory integration is solved by an analog control system in a spatially reified replica, or model of external space in an internal representations. It is an analog modulation of an analog reified motor pattern, as analogical computations taking place across a spatial medium. And perhaps the most significant feature of this analogical principle of sensorimotor computation is that it automatically scales up from single-celled to multi-celled organisms with no additional hardware required.

From Single-cellular to Multi-Cellular Creatures

The transition of this resonance motor system from single-celled to multi-celled organisms can be tracked in an interesting family of transitional creatures known as the *Volvocales*, and their single-celled cousin the *Chlamidomonas*, shown in Figure 4.2. The Chlamidomonas, Figure 4.2 A, is a flagellated creature like the Euglena, that exhibits phototaxis, steering toward light in low-light conditions, and away from the light when it gets too intense. The Volvocales are composed of multiple cells stuck together, each cell equipped with its own pair of flagella, all the flagella directed outward away from the center of the cluster. Some Volvocales, like the Gonium, Figure 4.2 B, are composed of from four to sixteen cells, each one very similar in appearance to the single-celled Chlamydomonas, as if some ancestral Chlamydomonas had developed a mutation in which the cells fail to fully separate after mitosis. In another Volvocale, the Pandorina, Figure 4.2C, the cells form a more orderly sphere of 16 cells, and another, Eudorina, Figure 4.2 D, forms a sphere of 32 or 64 cells arranged in a perfect spherical pattern, rather than being just randomly stuck together, thus marking the first stage of embryological
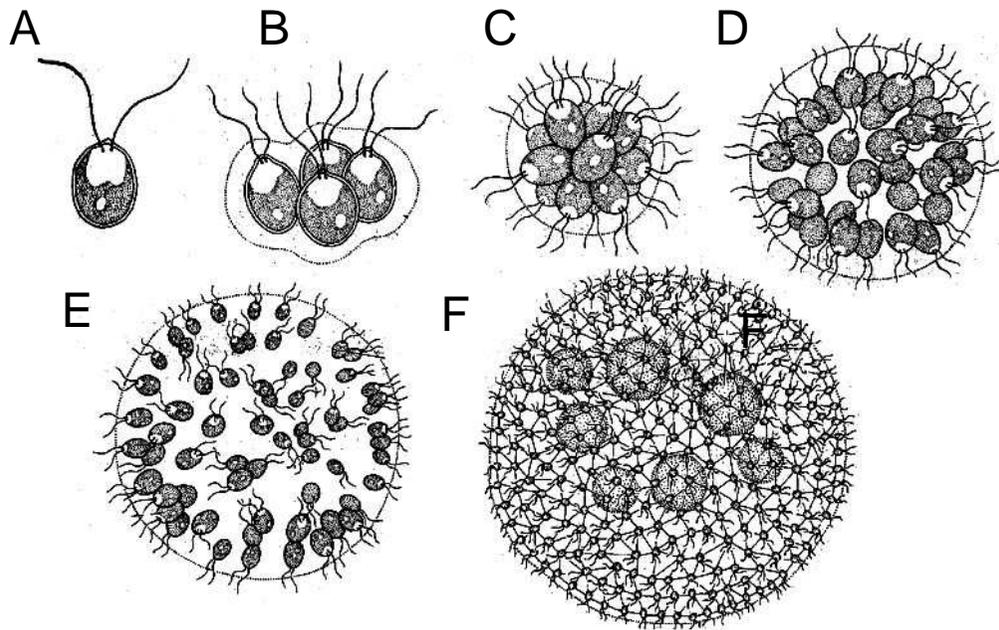
Figure 4.2. A: Single-celled animal Chlamydomonas, and a series of multi-cellular Volvocales with increasing numbers of cells; B: Gonium, C: Pandorina, D: Eudorina, E. Pleodorina, and F: Volvox. Although composed of a conglomeration of individual flagellated cells, the flagella of these compound organisms wave in synchrony as a single organism.

morphogenesis, the orderly division of one cell to produce a number of cells organized in a defined body plan. The next two genera of Volvocales, Pleodorina and Volvox, Figure 4.2 E and F, exhibit another advance into multi-cellular organisms, cell specialization. Whereas in Eudorina, every cell can, and usually does, produce a whole new organism by mitosis, in Pleodrina and Volvox, only relatively few cells on one side of the organism can reproduce, and in one species of Volvox, very few cells can reproduce, and those that can, never develop flagellae, having specialized for the role of reproduction exclusively. The Volvocales therefore exemplify the earliest stages of multi-cellular evolution, and they also illustrate the earliest stages of inter-cellular synchronization in sensory and motor function, because all of the volvocales exhibit the kind of phototaxic behavior performed by the single-celled Chlamydomonas.

Let us return to the Chlamydomonas. Unlike the Euglena, this creature actually has two flagella instead of just one, and they sprout from the anterior end of the organism, next to each other, and make mirror-symmetric waving motions somewhat like a swimmer's breast-stroke, to promote locomotion in the anterior direction. So here we have two flagella that are physically separated, and yet act in symmetrical synchrony, obviously coupled, functionally speaking, through the cell membrane or cytoplasm, without any neurons or wires or mechanical

connections, and that synchronous swimming pattern is responsive to the direction of light. (Cells of old cultures often exhibit disturbed synchrony between their flagella, with the result that swimming is erratic, cells frequently tumbling and turning uselessly in small circles, so the invisible synchronizing mechanism can be disrupted, with negative consequences for the organism.)

Now let us consider the ancestral Chlamydomonas whose failure to completely separate on mitosis founded the original Volvocale lineage. If the motion of its flagella are indeed synchronized by some kind of electrochemical oscillation through the cell membrane or cytoplasm, then this oscillation would also naturally tend to synchronize the electrochemical oscillations of the stuck-together cells. In other words, the very same mechanism that synchronizes the two flagella on a single Chlamydomona, could naturally extend to a synchronization of all the flagella on the compound organism, without having to evolve a new synchronization mechanism simultaneously with the spontaneous mutation that caused the failure to separate. The beauty of harmonic resonance is that it is so simple and primal of a process, that it naturally extends to oscillations in the compound creature composed of multiple cells, by the principle of entrainment of oscillations in similar oscillators. The remarkable aspect of Volvocale behavior is the perfect global synchrony between the motions of the flagella of its component cells, that somehow coordinate their direction of cyclic oscillation to conform to a global motor plan that allows the complete composite organism to behave as a single individual, that exhibits the same basic phototaxic behavior as the single-celled Chlamydomona. The coherence and synchrony of individual cells united into a single multi-cellular organism is seen most clearly in the Volvox, the most advanced of the Volvocales, a perfectly spherical organism made up of up to about 500 individual cells, arranged in geodesic symmetry, all of them synchronized and coordinated in the beating of their pairs of flagella, all in the absence of any kind of explicit synchronizing mechanism such as neural connections or mechanical linkages. Harmonic resonance is an extraordinary force for the emergence of global synchrony in identical resonators, at either the single-cellular, or multi-cellular level, and that is why nature makes use of this beautifully simple principle of harmonious interaction as the primal and primary principle of co-ordination and synchronization in organisms large and small.

The principle of harmonic resonance can also be invoked to explain the functioning of the simplest nervous systems in primitive creatures like the Hydra, discussed in Chapter 1. How could one possibly account for the structured and

coordinated motor patterns of the Hydra, given its totally unstructured homogeneous network nervous system? How does the tissue of the hydra know where to contract and where to extend at each moment in time, when performing a synchronized behavioral pattern such as somersault locomotion? The resonances in the Volvocales, in the absence of any nervous system, demonstrate the principles of resonance in the simplest of animals. Surely the earliest nervous systems would build upon that more primitive resonance principle, rather than replace it with something completely different with the emergence of an explicit nervous system. The homogeneous fishnet type of network of the Hydra's nervous system surely serves to amplify and modulate the more basic natural resonances of the Hydra's tissue of animal cells, that provide the original sensory stimuli and actual muscular contractions. In other words, the Hydra's network nervous system surely behaves as a resonator, like a musical instrument playing a sustained note, whose own natural resonances coordinate and modulate corresponding resonances in the tissue of the Hydra, and the pattern of those standing and/or travelling waves determines the patterns of posture and/or movement of the little creature.

Arthropod and Insect Locomotion

Further evidence in support of a harmonic resonance theory of neurocomputation can be found a little higher on the evolutionary ladder, in the patterns of locomotion of arthropods and insects. Millipedes and centipedes exhibit most clearly a wave-like pattern of motion of their legs, that surely must result from waves of electrochemical activity coursing down their spinal cords. As with the wave-like contractions of a swimming eel, the wave-like stepping pattern of a centipede is not just a simple wave, but one that is clearly modulated, to enable the creature to steer left or right, up or down, superimposed on the propulsive stepping undulations of its legs. And this walking pattern cannot simply be imposed top-down by a pattern generator in the creature's "brain", because the pattern of steps must adapt to the irregular surfaces and structures across which the creature crawls. Computing the appropriate leg deflection for each leg of the centipede as it walks and steers over irregular terrain while steering toward some sensory stimulus, poses a formidable control problem for any theory of sensorimotor function. A harmonic resonance mechanism naturally generates these kinds of wave-like patterns, and offers a simple mechanism for superimposing steering commands, and sensory feedback, on the propulsive undulations of a motor pattern generator, to define a single integrated sensorimotor plan of motor patterns modulated by sensory input.

Gallistel (1980) reviewed some of the theories that have been proposed to explain the wave-like motions of animals like centipedes and snakes and eels. Gallistel rejected the model of a simple reflex chain, where peaks of activation are passed along the spinal cord from anterior to posterior in sequence, like the progressive collapse of a line of dominos, because under ether, an earthworm contracts simultaneously along its length, which would be impossible for a reflex chain. Furthermore, an isolated nerve cord is observed to continue to oscillate electrically, like a snake that continues to writhe after it is chopped into pieces. Gallistel concludes that "*the nervous system is not, in fact, like a lazy donkey which must be struck ... every time before it can take a step. Instead, it is rather like a tempramental horse which needs the reins just as much as the whip.*"

The advantage of using a harmonic resonance principle for defining this motor plan is that it allows an immediate bi-directinal flow of information, both top-down from the "brain" to determine the direction and pace of the walking, but also bottom-up from each limb, to communicate its current posture back to the rest of the motor field. For example if one or more legs of the centipede are mutated, or injured, or temporarily bogged down, or snagged on some obstacle, the creature can react with a globally coherent and balanced motor response that takes account of that unplanned deviation from the standard walking template, while at the same time communicating the situation bottom-up back to the "brain" in case a change of plan is called for. In other words, the phase of the rotary wave that determines the phase of the stepping cycle for each leg, must be modulated not only top-down by a global motor pattern generator, but it must also be determined by somatosensory feedback from each leg, so that a leg that is bogged down and thus phase-delayed relative to the desired motor plan, will automatically lag the phase of its motor standing wave, which in turn will distort the whole global motor pattern, slowing down the phase of adjacent legs, which in turn slow down legs still farther away. In other words, the entire motor field is interconnected with bi-directional feedback forces like water seeking its own level in a closed vessel, every particle of water reacting continuously to any change in the quantity of water at every other point in the vessel

Amputation Experiments

The total interconnectedness of the motor patterns of the centipede has been revealed in a series of amputation experiments, where the removal of legs in various configurations leads to characteristic changes in the motor pattern of the remaining legs, in a manner that defies any simplistic explanation in terms of a

reflex chain, or stereotyped motor pattern template, and strongly implicates a harmonic resonance principle of motor control. Gallistel (1980, p. 83-85) reports that the centipede Lithobius normally moves its legs in "wave" form, each leg separated from the next by a phase-lag of about one seventh of a step, so that each "wave" covers about 6-7 legs. If the centipede's legs are amputated, leaving only six remaining legs, then the motor pattern adapts to this change of body plan by moving the remaining legs in the pattern of a six-legged insect, regardless of whether the remaining legs are contiguous, or separated by gaps of one, two, three, or more amputated legs in between. And if a further pair of legs is amputated, leaving only four, then the remaining legs exhibits the characteristic gaits of a four-legged animal, like a trotting horse. In other words, the more complex motor patterns of four and six legged locomotion are already pre-programmed into the motor pattern repetoire of the simplest of the arthropods, the centipede with its string of identical segments and simple wave-like walking pattern. Figure 4.3. is a copy of figure 4.6 (p. 84) from Von Holst (1980) .This is
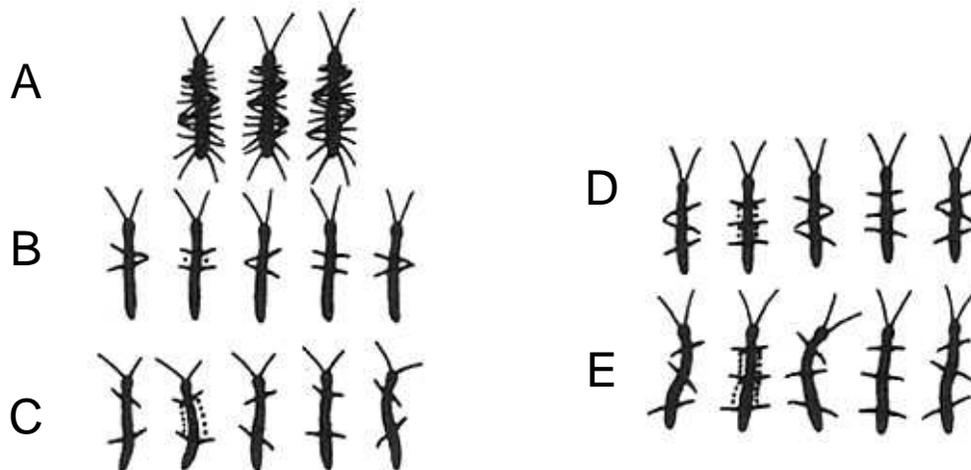

Figure 4.3. Phases from the running movement of the centipede *lithobuis* (from film records). A: Normal animal. B and C: after amputation of all pairs of legs except two. D and E: After amputation of all except three pairs of legs. (The dots in the second diagram in each series indicate the numbers of segments between the legs.)

evidence of the *multipotential pattern formation principle* characteristic of harmonic resonance, in which a very simple mechanism is capable of not just one pattern of motion, but a whole array of different patterns that can be evoked under different circumstances. A similar adaptability in insect locomotion was demonstrated by Bethe (Gallistel 1980, p. 83), who showed that a six-legged stick insect whose middle pair of legs is amputated, demonstrated a four-legged gait like that of a trotting horse. This multipotential adaptibility of harmonic resonance is an essential prerequisite for evolution in the first place, if the organism is to survive and adapt to random mutations and variations in its body plan.

In all these experiments a general rule was observed, that the smaller the number of legs present, the greater the phase difference between them. In more general terms this rule means that the processes in one ganglion are quantitatively dependent on the processes in all the other active ganglia. This interconnected coupling in turn implicates a harmonic resonance principle of locomotion.

Insect Locomotion

Arthropod evolution exhibits a progressive reduction in the number of legs, from hundreds in the milipede, and dozens in the centipede, to eight in the Arichnids, and to six in the insects, in each case adapting to the drastically altered body architecture with adaptive motor patterns that configure themselves to match the body to which they are attached. The centipede has basically only one gait, or pattern of stepping, and that is wave-like, although that wave pattern can be modulated in speed and direction, and even reversed for retreat. The six-legged insect, by contrast, exhibits an extraordinary six distinct *gaits* as it walks, as shown in Figure 4.4.. The legs of the insect are labeled as shown in Figure 4.4 A, and the plots on the left show the patterns of stepping motion of the insect's legs for the six gaits. The shaded rectangles represent times when a leg is in motion, swinging forward, the white rectangles represent times when the leg is in contact with the ground, pushing backward. On the right in the figure is the sequence of steps for each gait over time, to demonstrate the overlap between steps on the left and right sides. Not all insects exhibit all of these gaits, but examples of all these gaits are found across the insect world, and many insects are capable of several of these gaits. The gaits are listed in the approximate order they are observed based on the speed of locomotion, with the slower gaits at the top, and progressively faster gaits toward the bottom. The first gait, which might be called an *alternating wave* gait, is seen in slow browsing, with a wave of foot advancement from posterior to anterior on the right, alternating with a wave from anterior to posterior on the left. The next three gaits also exhibit posterior-to-anterior waves of stepping on left and right, with progressively increasing overlap or alternation between the left and right feet from Figure 4.4 B through D. These gaits are similar to the waves seen in centipede locomotion. Figures 4.4 B and C show how as the gait gets faster, the waves on the right and left sides no longer wait patiently until the other side finishes, but steps in overlapping waves on left and right.

Figure 4.4 E shows an interesting *alternating tripod* gait, that alternates between two stable tripod configurations with three legs on the ground, while the other

14

Insect Gaits

A   Alternating Wave Gait

—— L3 L2 L1 —— L3 L2 L1

R3 R2 R1 —— R3 R2 R1 ——

time ⟶

B   Single Overlap Gait

L1 — L3 L2 L1 — L3 L2 L1 — L1

R3 R2 R1 — R3 R2 R1 — R3 R2 R1

C   Double Overlap Gait

L1   L3 L2 L1   L3 L2 L1   L3 L2 L·
R3 R2 R1   R3 R2 R1   R3 R2 R1

D   Parallel Waves Gait

L3 L2 L1 L3 L2 L1 L3 L2 L1 L3 L2 L1
R1 R3 R2 R1 R3 R2 R1 R3 R2 R1 R3 R2

E   Alternating Tripods Gait

L2 L1 L3 L2 L1 L3 L2 L1 L3 L2
R1 R3 R2 R1 R3 R2 R1 R3 R2 R1

F   Running Gait

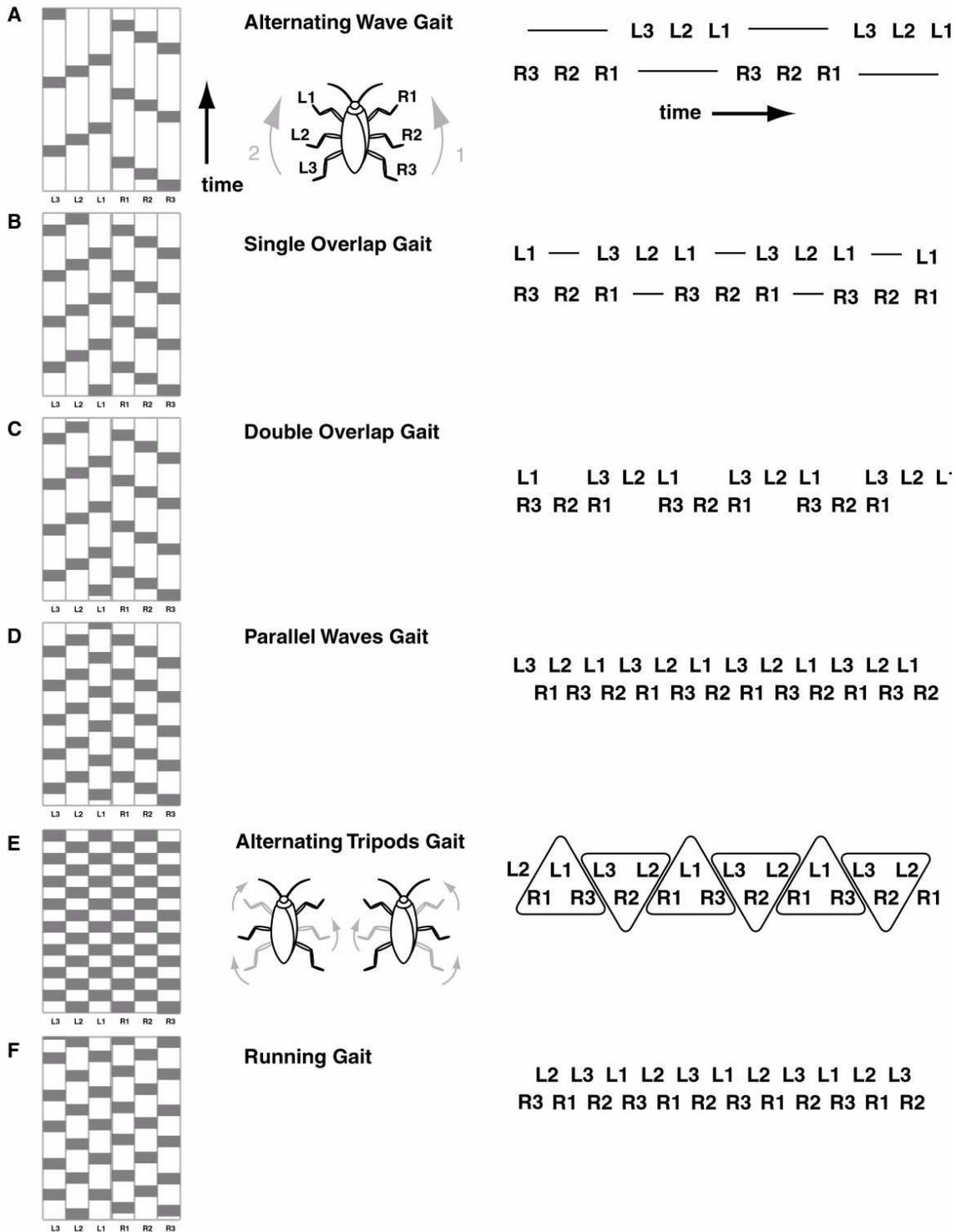L2 L3 L1 L2 L3 L1 L2 L3 L1 L2 L3
R3 R1 R2 R3 R1 R2 R3 R1 R2 R3 R1 R2

Figure 4.4. The six gaits of a six-legged insect. Most insects exhibit only a few of these gaits in their repetoire. The gaits are sorted by the order in which they tend to be used with increasing speed of locomotion, the early ones, A, B, C, are seen in slower movement, whereas the later ones, D, E, F, are seen in progressively faster running. The alternating tripods gaits, E, has a particular symmetry and is commonly found.

three legs swing forward ready for the next step. This is a particularly elegant and balanced gait, seen commonly in faster insects. And Figure 4.4 F shows a faster running gait in which the waves of leg motion exhibit a criss-cross diagonal striped pattern in the figure to the left, revealing interlocking waves of leg motions with two distinct components. Looking at the patterns on the right legs only in Figure 4.4 F, the diagonal patterns that progress upward to the left, (moving bottom to top in the figure) represent waves of leg motion from posterior toward anterior, like the pattern of Figure 4.4 A, whereas the diagonals progressing up and to the right represent waves of motion from anterior to posterior, interwoven with the waves in the opposite direction. The continuity of these diagonal rows of motion from the right to the left, and the other way, represent circular waves of leg motion that begin with a wave from posterior to anterior on the right side, flowing continuously into a wave from anterior to posterior on the left, that is, the waves travel up the right side and down the left, and round and round in circular repetition, while at the same time there are similar mirror reversed patterns going up the left side and down the right, like two counter-rotating circular waves that cause leg motions wherever they cross and thus interfere additively. These patterns are reminiscent of the kinds of rhythms seen in drumming, in which the left and right hand beats interlock in a variety of different patterns with abrupt transitions between discrete levels of interlocking patterns, which all exhibit the twin properties of symmetry and periodicity across tone and time.

The Gaits of a Horse

Evidence for a harmonic resonance principle of motor control is evident also in four-legged creatures like a horse. Figure 4.5.. shows the five gaits of a horse, or other four-legged creature, arranged, as before, in order of the speed of travel at which they typically appear. Figure 4.5 A shows the *walk*, which is similar to the insect walking pattern of Figure 4.4A, all the legs on the right side move from posterior to anterior, followed by the same sequence of the left legs. Figure 4.5 B shows the *trot*, an alternating gait in which diagonal pairs of legs are on the ground in alternating sequence. This is the four-legged equivalent of the insect's alternating tripod gait. Figure 4.5 C shows the *pace*, in which the two left legs alternate with the two right legs. Figure 4.5 D shows the *canter*, a three-phase pattern in which a diagonal pair of legs (in this case the left front and right rear) step together, followed by each of the remaining legs stepping in sequence, in a "this - both - that, this - both - that" kind of sequence, a motor pattern with a Waltzing rhythm. There are two alternative forms of the canter, called "left lead" versus "right lead" canter, depending on which diagonal pair of legs steps together

Horse Gaits

A

Walk

L1   R1

L2   R2

time

time →

B

Trot

C

Pace

D

Canter

E

Gallop

Figure 4.5. The gaits of a horse, plotted to the left, and illustrated to the right. The darkened hoofs represent the leg or legs that are stepping forward, the white horse-shoes represent legs standing on the ground.

and which step individually. Finally Figure 4.5 E shows the gallop, in which the rear legs alternate with the front legs in a two-phase front-and-back alternation.

Strogatz and Stewart (1993) observe that the patterns of gaits across different species with different numbers of legs, correspond exactly to the patterns of a set of coupled oscillators, with one oscillator for each leg. For example the four gaits

of a horse correspond to the patterns exhibited by four coupled oscillators, whereas the six insect gaits correspond to the patterns of six coupled oscillators. According to this analysis, there is one additional gait of the four-legged animal which is not seen in the horse's gait repetoire, and that is the four-legged hop, known as a *pronk,* and sure enough, there are several species of antelope or ungulates that exhibit this gait also. This analysis also extends to two-legged creatures and bipedal gaits, which exhibit the modes of two coupled oscillators, walking and hopping.

The significant aspect of a harmonic resonance principle of motor control is that these various gaits need not be hard-wired in any kind of rigid template or schema for each gait, but rather, they are emergent properties of a motor system that is reciprocally inter-coupled, in such a way that the motion of each limb has an effect on the motion of all the other limbs, with the result that the limbs automatically interlock in periodic temporal patterns in which each leg moves once in each cycle, and different patterns emerge spontaneously under different walking conditions. When the urgency of locomotion, or desire to move, is slowly ramped up, the lowest energy patterns emerge first, then progressively higher energy patterns, with discrete steps between a fixed number of discrete modes. And yet, although each gait is a discrete pattern, it is also fundamentally analog, and thus easily modulated for the purpose of going faster or slower, and steering left or right, and since a harmonic resonance system automatically adapts itself from moment to moment to the current configuration of all the legs, this kind of system also automatically adapts to unpredictable circumstances in real-time, such as injury or fatigue to one or more limbs, or encountering unexpected or irregular resistance to leg motion. This is presumably why nature favored a harmonic resonance principle for locomotion over a more stereotyped cam or template-like schema.

Centralization and Modularization of the Nervous Systems

There is a clear trend in the course of evolution of the nervous system from simple distributed toward complex centralized nervous system architectures. The reason for this trend is seen in the simplest centralized nervous systems in the evolutionary successors to the hydra, the hydromedusae, the earliest progenitors of the squid / octopus line. These creatures combine a distributed network nervous system like the hydra's, with a fast-action giant neuron reflex system for rapid escape. Hydromedusae are like hydra that swim instead of remaining stuck to the bottom. They propel themselves through the water by squirting water from

their mouth rhythmically, in a slow wave cyclical alternation of intake and exhaust during normal locomotion, or in powerful bursts for escape. The advantage of the centralized architecture is clearly evident in this creature. A noxious stimulus of sufficient magnitude from any point around the creature's body can trigger its emergency escape response, and yet that response, when fired, itself triggers a wave of muscular contraction, synchronized with a constriction of the mouth to increase the jet effect, alternating with an intake phase with mouth open. There is a many-to-one and one-to-many relation between the interaction of the peripheral and the central systems, which clearly exemplifies the principle of abstraction.

The nervous signal in the central system is very simple, just periodic pulses of electical energy in a linear resonator. But that signal is only useful or meaningful because of its ability to trigger travelling or standing waves of spatial pattern in the tissue, causing waves of muscular contraction in the pattern defined by the local phase. And the central system is useful or meaningful as a sensory system only because local sensations picked up by sensory organs anywhere on the creature's surface can potentially trigger a global escape response. The one-to-many, and many-to-one intercoupling between the central and peripheral systems is provided by spatiotemporal waves of oscillation in both sensory and motor representations.

The value of an abstract neural representation, like the one representing the escape response, is in direct relation to its efficiency in triggering that response, and thus it will have additional value if it can represent more than just a single stereotyped response, but pick from a wider repetoire of basic movements modulated by sensory input. It is also essential to keep the periodic pulses of the central system synchronized with the cycles of contraction of the musculature that it stimulates. If the contraction is slowed down for any reason, whether due to local injury or fatigue, it is best for the central nervous system to detect that response lag, and compensate with slower oscillations, or perhaps compensatory asymmetry in the motor pattern, so the central nervous system needs continuous feedback from the periphery to keep it in synch with external reality. This is where a harmonic resonance principle is so essential. Like a parent pushing a child on a swing, the pulses of thrust must remain in perfect synchrony with the swinging child, a task which humans find natural and intuitive, due to the resonance principle of our nervous systems. In fact, the very urge of children to swing rhythmically on swings and rocking chairs, is evidence of a harmonic resonance in their brains.

A general principle in the relation between the central and peripheral nervous systems activation can be characterized as follows. The central system emits a powerful pulse of electrical energy, then it waits in a refactory mode until it gets back an "echo" from the periphery acknowledging receipt of, and successful execution of the commanded contraction, before sending out the next pulse. There is a dynamic standing wave relation between the oscillations in each system, even though one is an abstract linear antenna, while the other is a volume of spontaneously resonating tissue in which spatiotemporal patterns are painted in three-dimensional space. This relationship is demonstrated in the principles of many musical instruments. For example the rude "raspberry" made by a trumpeter's lips, acts as the central nervous system, its energetic vibration sets up the initial waves in the trumpet, but with the very first reflected wave coming back from the far end of the trumpet, a beautifully symmetrical and periodic standing wave establishes itself in the three-dimensional volume of the instrument, and a harmonious tone ensues, as the trumpeter's lips are seduced into vibrating in synchrony with the perfectly periodic sound from the trumpet's resonance.

Another significant property observed in the evolutionary development of central nervous systems is a *modularity*, or *multiplicative tendency*, a natural tendency to spontaneous form repeating copies of the same pattern elements. The principle is clearly evident in morphogenesis, as seen in the patterns of plant and animal forms, like sunflowers and starfish, fiddle-head ferns and centipedes. And the same kind of modularity is also in evidence in the periodic patterns of nodes, or ganglia, observed along the spinal cord in vertibrates. If the central nervous system of vertibrates operates on the principle of harmonic resonance, as I propose, then this periodic or modular architecture would have a natural tendency to resonate in modular standing waves that reflect the modular or multiplicative architecture of the nervous system itself. This principle of multiple similar resonances in a series of coupled, near-identical resonators, reveals a powerful organizational principle in nervous function that can be explored with a thought experiment.

The resonances in a simple linear spinal cord, i.e. a cylinder of spontaneously resonating tissue, without periodic ganglia would be similar to the resonances in a cylindrical cavity, the most basic of which subdivide the linear dimension of the resonating cavity into periodic intervals of alternating motion. The first harmonic resonance represents an alternation in time, with a wave travelling one way alternating with a wave travelling in the other, a back-and-forth reciprocal motion

along the axis of the cylinder. The second harmonic is a 2x multiplication of that pattern in both space and time, with pairs of half-waves propagating from the ends to the middle, then reflecting off each other back out to the ends, two half-waves balanced against each other at double the frequency of the fundamental. The waves in this second harmonic mode are constrained to remain mirror-image replicas of each other, because if one half-wave were to be attenuated by some random resistance at some point in the resonator, then it would no longer have the momentum to completely reflect its counterpart, and thus its counterpart would also tend to lose that same component of motion when they collide at the center, automatically transfering energy from the stronger wave to the attenuated one, exactly in the place and time where that wave was lacking in energy.

This principle can be demonstrated in an acoustical model of the phenomenon. Consider a cylindrical flute, energized by air blowing across its mouth, capable of resonating at any frequency which is a harmonic of its fundamental, as suggested in Figure 4.6..A, showing the amplitude functions of the first six harmonic
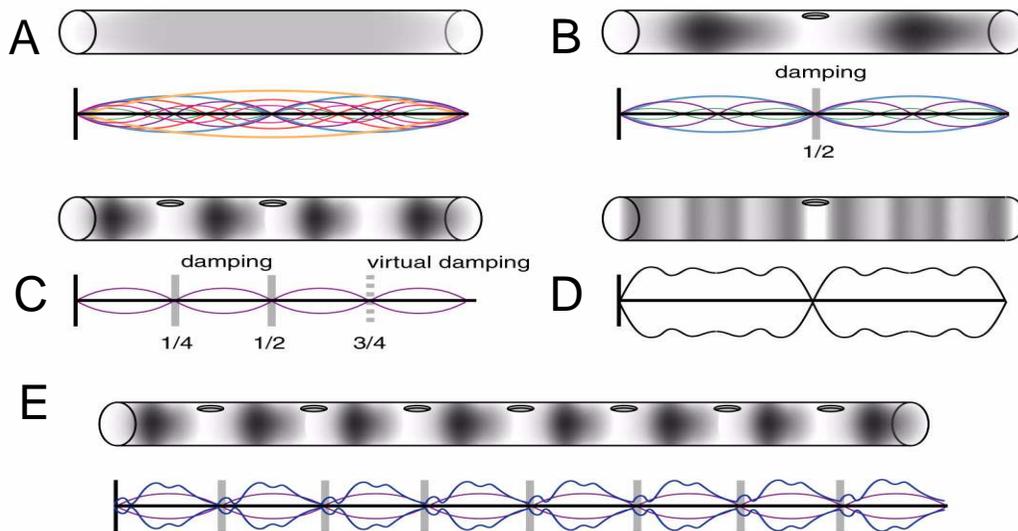

Figure 4.6. Modularization of the nervous system demonstrated with an acoustical analogy. A: A linear tube supports multiple resonances. B: An open hole at the half-way point damps the odd harmonics. C: A second hole at the one quarter position damps the second and sixth harmonics. D: Even more complex waveforms are constrained to mirror-symmetry across the central node. E: A flute with a periodic array of open holes is constrained to standing wave patterns that also repeat in periodic intervals, either a simple fundamental, (purple) or a more complex compound waveform (navy). But the waves are not merely dumb copies, they are causally interconnected to act as a whole.

waveforms for that resonator (plotted in colors orange, blue, red, purple, pink, green). An open hole at the center of the tube, as suggested in Figure 4.6 B, would promote a node of vibration at that central point, because the open hole short-circuits any standing wave with an anti-node centered at that location, which

includes the first harmonic, along with the third, and fifth, that is, the odd harmonics on the fundamental. With this open hole, the second harmonic resonance becomes the new fundamental of this now bimodal resonator, it is now the lowest energy note that emerges most readily from the resonator. This central node has turned the half-waves into mirror images of each other, reflecting back and forth across the central nodal point as if bouncing off a mirror in both directions. But these symmetrical half-waves are not merely similar in appearance, they are coupled in a relationship that constrains them to remain identical to each other energetically. For example if a second hole is opened at one quarter the length of the tube, as shown in Figure 4.6 C, this open hole will promptly damp any harmonic with a strong anti-node at that location, including the second harmonic (blue), which has an amplitude peak right at that spot, as well as the sixth harmonic (plotted in green) which is also damped. This damping affects the second harmonic wave not only there at the open hole, where the acoustical short-circuit is in effect, but it also damps its counterpart at three quarters the length of the tube, a mirror-image reflection of the node at the one quarter position. The hole is robbing energy from the resonance continuously, but robbing only energy at one specific frequency, the second harmonic, (and the sixth) and from two specific locations in the standing wave, at distances one quarter and three quarters. But since the energy leak is actually through the hole in the one quarter location, there is a continuous flow or leak of energy from the three quarters point in the tube, across to the other side of the center and out the hole at the one quarter point, because any spontaneous resonances that happen to emerge at this frequency will fail to be reflected back from the other half of the tube. The damping due to the hole at the one-quarter location creates a *virtual damping* at the mirror-symmetric three-quarters point, as if there were an open hole at that point also. A similar damping occurs with the sixth harmonic, whose damping at the one-quarter point effectively creates a weaker virtual damping at all the anti-nodes of the sixth harmonic in both halves of the tube, although the magnitude of this damping is considerably weaker than that of the second harmonic, because the open hole damps only one of the six anti-nodes of the sixth harmonic, whereas that same hole damps a full one-half of the two anti-nodes of the second harmonic.

The same principle applies also to more complex waveforms containing component higher harmonics, as suggested schematically in Figure 4.6 D. Even these more complex compound waveforms are constrained by the open hole at the center of the flute to patterns that are mirror-symmetric across the center, so

that they can bounce off each other with perfect reciprocity. This is the principle of modularity, a characteristic feature or property of harmonic resonance.

Modularity is not restricted to the bimodal resonator split into equal halves by a central damping point, but the same principle can be generalized to a periodic array of holes at equal intervals, which also subdivide the resonator into equal resonators, which in turn would promote a fundamental frequency (purple in Figure 4.6 E) whose wavelength exactly matches the spacing of the holes, but with the same interconnected property of the bimodal resonance expanded to multimodal reciprocal reflections. Although each standing wave in each of the nodal intervals vibrates independently as if it were by itself in a single-antinode cavity, they are also subtly interconnected energetically, such that if some component frequencies are amplified or damped in any one of the identical resonators in the chain, there will be a continuous leak or flow of energy from the the other resonators toward the damped point, which in turn would establish virtual damping at the corresponding locations in their copies of the wave. The result is that whatever the waveform that emerges from this periodic array resonator, its waveform exhibits a strong tendency to be identical in each nodal interval, as suggested by the blue trace in Figure 4.6 E, and that waveform is shared among all of the resonators in a distributed fashion. Any additional damping that might occur in any of the segments, for example due to the opening of additional holes, would create a notch in the waveform corresponding to the location of that hole, and that notch due to damping in one segment is replicated in every other segment with a corresponding virtual damping. Thus the pattern of resonance in this periodic resonator is causally coupled across the array, each pattern intimately coupled with every other pattern in the array. This principle of modularity, or multiplicative tendency, is exploited by nature as a means of coupling, or synchronizing the patterns of representation in sensory and motor systems in a periodic array-like architecture of coupled resonators.

Beads On A Straw

The architecture of the vertibrate spinal cord is shaped not so much like a uniform cylinder, but more like a cylinder with periodic nodes, or ganglia, along its length, strung somewhat like beads on a straw, as suggested schematically in Figure 4.7 A. In a resonance neural architecture this configuration can be expected to establish nodes of resonance at periodic intervals to match this periodic architecture. But the prominent swellings at each ganglion promote a different kind of standing wave at those locations, more similar to the spherical resonances
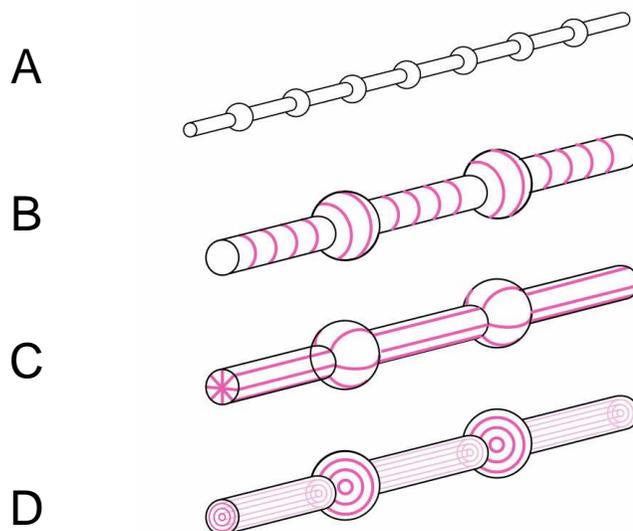
Figure 4.7. A: The topological archititecture of the vertibrate spinal cord is somewhat like beads threaded on a straw, a cylinder with periodic nodes, or ganglia. B through D: Some of the many possible standing wave patterns that would spontaneously emerge in a self-amplifying resonator that had this geometry.

of a spherical resonator, as opposed to the cylindrical resonances along the spinal cord itself. A spherical resonator has many more possible standing wave patterns than a cylinder, allowing for more possible patterns of sensory or motor encoding in each segment. Consider the basic modes of resonance of a spherical resonator, shown in Figure 1.18 A through D in Chapter 1. Each of these resonances could appear spontaneously in a self-amplifying spherical resonator, even one connected to other similar resonators by the resonating cylinder of the spinal cord. Some of the resonances in the spheres would couple with corresponding resonances along the spinal cord. For example Figure 4.7 B shows linear resonances back and forth along the spinal cord segments, interacting with similar one-dimensional lateral standing waves through the node, as if that node was part of the cylindrical spinal cord. Other modes of resonance are totally independent of, or invariant to linear resonances in the spinal cord. For example Figure 4.7 C shows radial resonances. These radial resonances occur orthogonal to the linear resonances, and thus would be entirely un-influenced by the linear resonances. Figure 4.7 D shows concentric, or "s-mode" standing waves in the spherical nodes, and there are additionally a number of rotational resonances with wave rotations in various directions. These additional modes of resonance offer additional degrees of freedom which can be employed for spatial representation in sensory and motor systems as explained below. Each of these standing wave resonance patterns would radiate its own characteristic wave outward into the

surrounding tissue, where these periodic patterns are projected onto muscles that contract based on the phase of the wave that they detect.

Putting Resonances to Work

Consider the motor control challenge that arose during the evolutionary progression from a millipede, with large numbers of very tiny legs, toward a centipede with a smaller number of somewhat longer legs, to an insect with just six legs but each very long with multiple segments. As the legs get longer they must get less numerous in order to avoid collisions with adjacent legs. And they gain more degrees of freedom of motion, especially as they grow additional segments. The motor signals to a centipede's legs can be fairly simple, a wave of deflection not so different than the waving of the cilia of the paramecium. But the legs of the centipede each have two degrees of freedom, forward / backward and up / down, along with an "up-forward-down-back" propulsive cycle for locomotion, as shown in Figure 4.8 B. This additional degree of spatial encoding can be
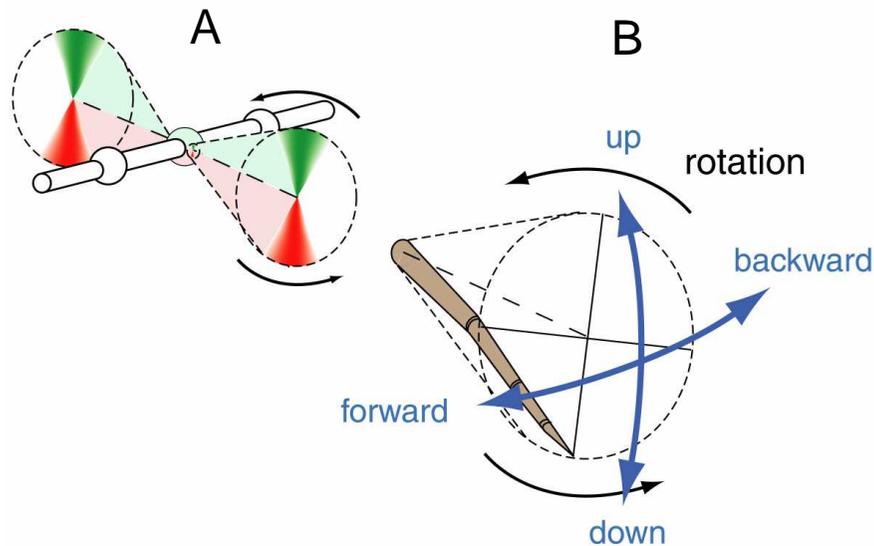

Figure 4.8 A: The degrees of freedom of a centipede's leg, forward, backward, up, and down, along with a rotational pattern used in locomotion, up-forward-down-back, can all be encoded with a rotating standing wave pattern in the ganglion, whose direction of rotational phase controls the angle of deflection of the leg.

provided by spherical resonances that represent the walking cycle, while resonances along the spinal cord can serve to synchronize and coordinate the resonances in the individual ganglia. I cannot say exactly which of these almost infinite possible standing wave patterns are actually employed in the sensory and motor functions of vertibrates, but we can discuss some of the possible resonances that might be employed, to illustrate how resonances can serve to

express complex spatiotemporal patterns in a globally integrated dynamic mechanism.

Hypothetical Model of Vertibrate Motor Control

Figure 4.8 A shows a cyclic oscillation through a ganglion of the spinal cord, whose phase represents the current phase of the stepping cycle at that point in the spinal cord. The two dimensions of the stepping cycle are easily encoded in spherical harmonics, and the phase from node to node is communicated by travelling waves along the spinal cord, lawfully time-lagged from node to node. The spinal cord need only communicate one dimension of information, the phase of the stepping cycle, and that simple one-dimensional synchronizing signal can synchronize an array of more complex three-dimensional resonators in phase with each other's patterns along the spinal cord. This kind of rotational standing wave resonance could explain the synchronized patterns of rotary motions of a millipede's legs.

As the short simple legs of the millipede evolved into the longer compound legs of the centipede, the same resonance architecture can be adapted to express the more complex patterns of motion required to control the individual segments of each leg in synchronized motion. The extra dimension of radial distance along each leg, can be encoded by a radial pattern of standing waves in the central nervous system, like the s-mode standing wave resonances of a spherical resonator. The general principle here for expressing the additional dimension of control is the same as the principle outlined above, where the central nervous system emits an abrupt pulse of electrical activity which propagates outward in all directions peripherally, to be reflected back from the terminals of the nervous system back to the central nervous system. Like the principle of echolocation used by bats, this principle can be used to map out the peripheral nervous system, and to build an analogical mirror-image replica of it back in the central nervous system.

Figure 4.9 A. I shows a simplified model of the nervous system of a centipede with segmented legs, each ennervated by a central nerve running down that leg, with nodal points disposed at intervals along the leg, corresponding to the series of joints, each of which offers still more degrees of freedom of motion. Imagine a powerful pulse of nervous energy that begins at the junction point where the spinal ganglion meets the nerve from each leg. That pulse would propagate down the nerve of the leg, sending back echos, or reflections, as it passes each node along the leg, as suggested in Figure 4.9 C through E. A listener, located at the nerve
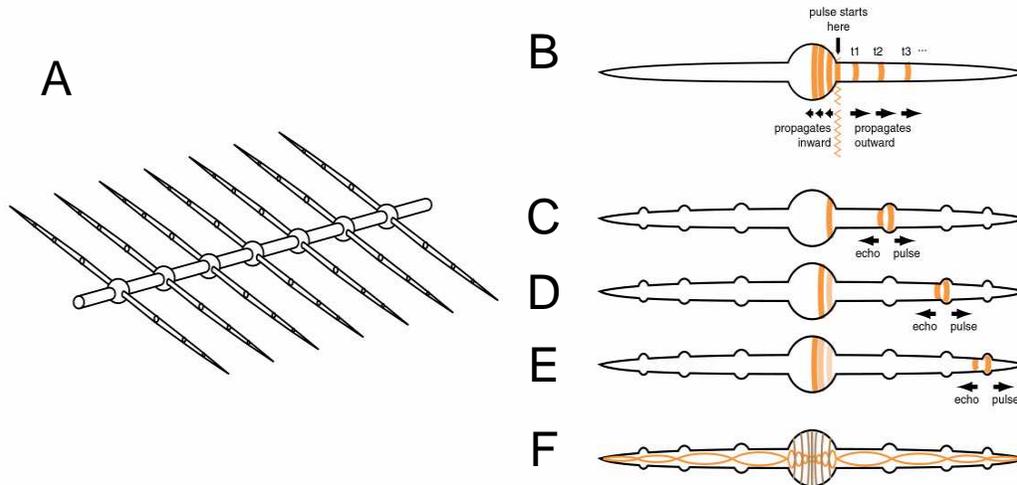
Figure 4.9 A: An idealized model of the centipede's nervous system, with nerves for each pair of legs projecting from the vertibral ganglia. B: A pulse of electrical energy starting at the nerve root, (C, D, E...) propagates outwards as a centrifugal wave, and inwards as a centripetal wave, sending back echos as it passes through the nodes. F: Cyclic pulses establish coupled, mirror-image reflected standing waves in the nerve and the ganglion.

root, listening to the pattern of echos returning from the leg, could determine the architecture of the segmented nerve, and thus of its segmented leg, by the segmented pattern of returning echos.

Now imagine that the centrifugal pulse that propagates from the root of the nerve to the tip, is matched by a centripetal pulse travelling in the opposite direction, from the nerve root towards the center of the spherical resonance of the ganglion, as shown in Figure 4.9 B, but with a considerably slower propagation rate, so that the centripetal wave reaches the center of the ganglion just as the centrifugal wave reaches the tip of the limb nerve. What we have is two mirror-image waves sweeping outward from the nerve root in synchrony. If the speed of wave propagation is very much slower in the ganglion than it is along the nerve, then these two mirror-image waves are presented at different spatiotemporal scales, and yet they remain in dynamic balance against each other. The centripetal sweep is a miniature copy of the centrifugal one, and if the speed of propagation declines in nonlinear fashion toward the center of the ganglion, that would define a nonlinear shrinking spatial scale as discussed in the previous chapter. The spatiotemporal similarity of these two waves in different media offers a means for plotting the spatial pattern of the limb as a corresponding spatial pattern in the ganglion.

The nerve that runs along the leg has little nodes or ganglia at each segment, that are like a miniature model of the ganglia along the spinal cord, and operate by

similar principles. As the centrifugal impulse passes through these nodes, it sends back a powerful echo that records the pattern of nodes in the limb nerve. As the pattern of periodic echos returns from the limb, those echos can be plotted in the central nervous system at the location of the centripetal wave, at the time of the returning echo, just as returning echos are plotted on a radar scope by an electron beam that sweeps in a pattern similar to that of the projected radar beam in external space. The periodic echos in time plot a spatial pattern of traces disposed radially in the ganglion, corresponding to the radial pattern of nodes along the legs. Now if the centrifugal pulses are repeated at intervals timed to the return of the last echo, this will establish a pattern of radial standing waves in spherical shells in the spinal ganglion, as suggested in Figure 4.9 F, to match dynamically similar patterns of standing waves along the nerve of the leg. This establishes a map, or representational framework coupled with the standing waves in the nerve that it models, at a scale that is proportional to the difference in propagation velocity, and this map can be used to encode the posture or motion of the leg.

Each joint of the leg is equipped with proprioceptive sensors that sense the degree of flexion or extension of the joint, in two dimensions at each moment of time. Now let us imagine that the signal from these deflection sensors is used to accelerate or retard the speed of propagation of the centrifugal waves through the nerve at that location, by an amount proportional to the degree of deflection. This would serve to deflect the direction of propagation of the waves travelling along the nerve, retarding them on the side where contraction is sensed, and advancing them on the other side, as we saw in the case of the spermatozoa model of Figure 4.1, and this has the effect of bending the whole wave in the nerve into a curve. Since the resonances in the nerve are coupled with those in the ganglion, this deflection in turn would distort the standing wave pattern in the ganglion too, providing an explicit spatial model of the posture of the limb at any time.

This principle is demonstrated in Figure 4.10 showing the distortions of the standing waves in a peripheral nerve when its limb is deflected, and how that distortion is reflected in a corresponding distortion of the standing waves in the spinal cord. Bending the whole leg coherently forward, bends the standing wave uniformly at each node, thus warping the whole standing wave pattern as it resonates in the nerve, sending asymmetrical return echo pulses back to the ganglion, where those pulses paint out a correspondingly distorted standing wave that mirrors the pattern of deflection of each of the joints in the limb. An analogical spatial representation for the purpose of performing spatial computations in the
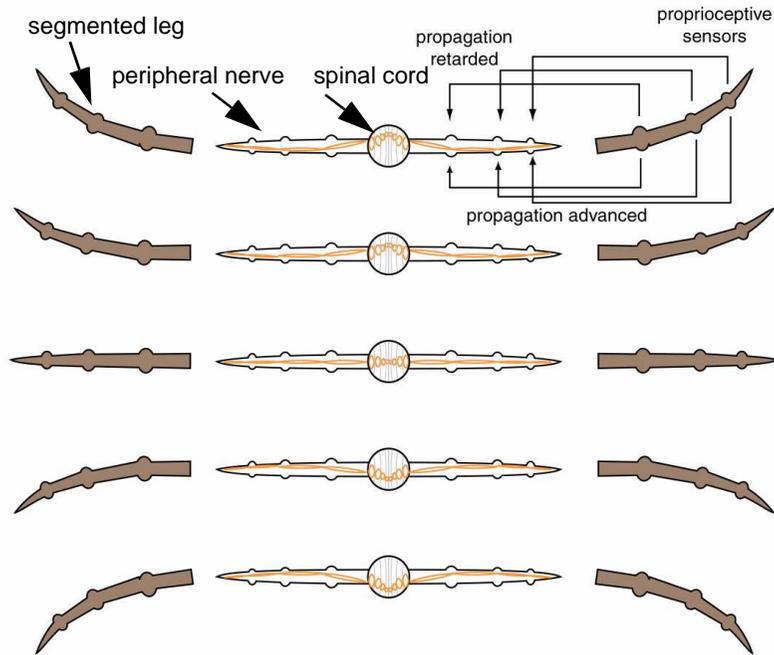
Figure 4.10. Proprioceptive sensors in each joint of the limb transform sensations of extension and compression to signals that advance and retard the speed of wave propagation in the local part of the nerve. A coherent distortion of the whole limb bends the standing wave in the nerve, and this in turn bends its mirror-image counterpart in the ganglion, which thus serves as an internal model of the external posture of the limb.

spatial medium of the nervous system. More generally, it is possible to create a harmonic resonance mechanism whose standing wave pattern duplicates in mirror-image fashion the spatial pattern of deflection of the limb, in an analogical, or quasi-pictorial spatial model of the limb duplicated in the volume of the central nervous system. The exact coding scheme actually employed in vertibrates like the centipede is merely conjecture at this point. The purpose of this thought experiement is merely to suggest how a harmonic resonance could in principle serve to construct analogical spatiotemporal models, or effigies, of the limbs that they control, and how the modularity of harmonic resonance offers a mechanism for coupled spatial patterns. However the exact coding scheme that is actually used by vertibrates could be easily determined through electrophysiological recordings, once it is clear that it is the phase of oscillation that provides the significant signal to be observed. This hypothesis is testable neurophysiologically.

The advantage of an explicitly spatial principle of analogical representation is that it allows explicitly spatial computational interactions between the standing waves in the representation. For example, spatiotemporal interactions between the standing waves representing the left and right legs controlled by each ganglion could be synchronized by spatial interactions between their corresponding standing waves in the ganglion, to produce coordinated, symmetrical patterns of

motion in the two opposing legs, like a swimmer's breast stroke, as suggested in Figure 4.10, where the standing wave patterns in the spinal cord interact at the center where they meet. In fact, exactly this same principle of symmetrical motions coupled by standing wave resonances is seen already in some of the very simplest organisms, the flagella of the swimming Chlamydomonas.

Motor Control in Cerebrate Animals

A harmonic resonance theory of motor control seems clear enough in simple creatures like a centipede, with its identical series of legs moving in phase-lagged copies of the same motion. But what of the cerebrate creature, beginning with worms and centipedes, whose frontal ganglia are considerably larger than all the others, the first step towards a brain. What kind of processing takes place in this oversized frontal ganglion? The modularity principle in harmonic resonance theory suggests that the relation of the "brain" to the rest of the nervous system, is similar to the relation of the spinal nervous system to its peripheral nerves, which is a cyclic reciprocal reflection against each other in harmonic resonance. Pulses of electrical energy triggered at the boundary where the "brain" and spinal cord meet, propagate simultaneously down the spinal cord, and at the same time up into the brain, where the echo returns received back from the spinal cord are painted out in a spatiotemporal sweep, creating a mirror-image replica of the pattern of the spinal cord as a model in the brain, sculpted out of electrical standing waves. In the case of the centipede, the standing wave pattern in the "brain", or frontal ganglion, would be a mirror-image reflection of the chain of ganglia of the whole creature, as suggested in Figure 4.11 A. Of course the speed of wave propagation in the brain would have to be considerably slower than that in the spinal cord, in order for the standing wave pattern to fit into the smaller dimensions of the brain.

The periodic pattern of echos returning from the chain of ganglia in response to a single centrifugal pulse, are painted out in sequence as a spatial pattern by the centripetal wave propagating up into the brain. This pattern of echos in turn can be used to lay out a pattern of nodes in the brain representation, between which a self-amplified standing wave can spontaneously emerge, creating a functional replica not only of the spatial pattern of the spinal cord and its periodic ganglia, but also of its resonant characteristics.

The brain-copy of the resonance of the ganglia would also include a copy of their resonances with their peripheral nerve, creating miniature traces of the limb nodes along each leg in the brain representation, reconstructing a spatial skeleton of the
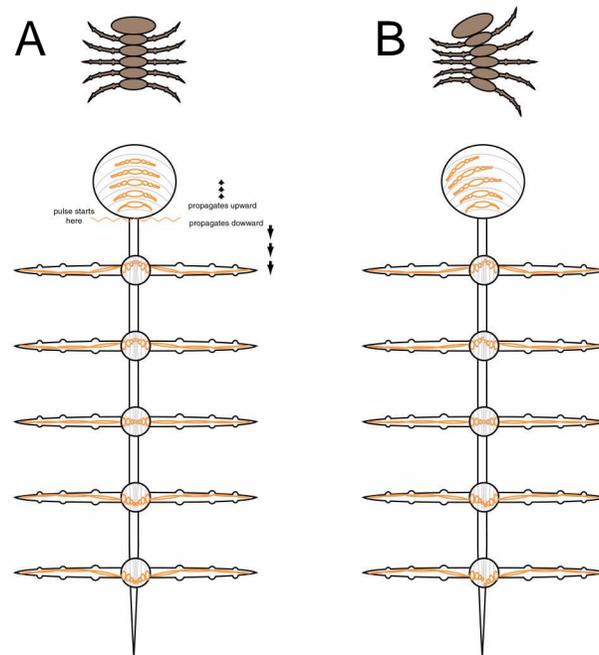
Figure 4.11 A: An electrical pulse, starting in the centipede's "brain" stem, propagates simultaneously down the spinal cord, and upward into the "brain". The periodic pattern of echos returning from the ganglia paint out a periodic spatial pattern in the creature's "brain", which in turn establishes a pattern of standing waves that mimic the dynamics of the spinal cord and peripheral nerves. B: Modulation of the global pattern in the "brain" warps that standing wave representation, for example to turn left, and that warp in the body image in the "brain" in turn warps the standing waves in the nervous system, causing the creature to actually turn left.

body in a spatial replica in the brain. In fact, the resonance goes one step farther, because the pulses emitted by the peripheral nerve at the center of each limb, propagates out radially through the limb, reflecting back from the muscle tissue enervated by that nerve, creating an echo of the outward pulse reflecting back from the outer surface of the enervated muscle, and this little echo would also be replicated in the spatial model of the body in the brain (not shown in Figure 4.11), where it would be plotted as an outer shell surrounding the replica of the peripheral nerve, with cyclic waves propagating radially from the periphery to the central nerve and back out again. In other words, what is constructed in the brain is a standing wave model of the body, complete with a spinal cord connecting periodic ganglia, with peripheral nerves connecting periodic nodes, with a peripheral body surface, all pulsing in-and-out in cyclic repetition, a dynamic spatiotemporal replica in the brain of the complex hierarchy of resonances pulsing through the nervous system and musculature. And that dynamic replica of the body in the brain remains functionally coupled to the body that it represents, such that changes in the sensory signal at any point in the body has immediate effects

at the corresponding location of the brain map of that part of the body, just as changes in the brain model of the body have immediate effects back on the body.

For example a global command might be imposed on the brain map for the creature to turn left as suggested in Figure 4.11 B. This would require a phase-lagging of the standing waves at some points, and advancing them at others, in order to curve the body to the required posture for a left turn. The "turn left" thought takes its meaning from the fact that it is capable of imposing a "turn left" posture on the brain's map of the body, and since this body map is dynamically coupled to the nervous system with which it is resonating, the phase modulation will be communicated from the brain to the spinal cord, where it will phase-lag the left side of the body while advancing the phase of the right, subtly warping the cyclic motion of every leg in accordance with a globally synchronized pattern.

Cerebral Cortex and its Maps

The modularity, or multiplicative principle of harmonic resonance also accounts for the multiple maps observed in the cortex in higher mammals, often disposed in mirror-symmetry across a sulcus. The largest such symmetry is the symmetry of the two cerebral hemispheres, coupled through the corpus callosum, suggesting a lateral left/right resonance reflecting back and forth across the medial plane. The next is the symmetry across the central sulcus, with the somatosensory homunculus on one side, and a mirror-image motor homunculus on the other side. In fact, the sensory / motor split continues all the way down the spinal cord, across the dorsal / ventral dimension, suggesting the most primal resonance of vertibrates as a periodic oscillation of sensory-motor-sensory-motor, oscillating in the dorso-ventral direction along the entire spinal cord and brain. There are also coupled oscillations between the various cortical maps, such as the primary, and secondary, and tertiary visual and somatosensory corticices, many of which are spatially adjacent and aligned in mirror symmetry to each other, suggesting a cortical oscillation back and forth across that axis of symmetry.

While the present theory does not predict with any precision exactly how these maps are organized or interconnected, the theory of harmonic resonance in the brain does make a number of specific predictions. It predicts that the phase of cortical oscillation carries the essential information of spatial location, and that movements of a stimulus across the visual field, or tactile stimulus across the skin, will be found to correspond to some waveform shifting in phase along with that translation. The theory predicts that adjacent, mirror-symmetrical cortical maps, starting with the primary somatosensory and motor cortex areas, will exhibit

phasic sweeps of electrical activity going back and forth symmetrically across the symmetry axis that joins them. More generally, the harmonic resonance theory predicts that the electrical activation of the cortex is synchronized to a universal phasic resonance, of which the oscillations in individual cortical areas or individual neuroanatomical structures are higher harmonics. And most generally still, the harmonic resonance theory predicts that the spatial patterns of our experience correspond directly to spatial patterns in our nervous system, explicitly painted out in a cyclic resonance in the form of spatiotemporal standing waves, which serves to couple all the individual parts of the computational mechanism of the brain into a single integrated system in which information is exchanged continuously and reciprocally, bottom-up, top-down, left-right, front-back, in parallel between the various different brain areas.