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# Network thermodynamics revisited

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## Abstract

Modeling provides a bridge between the natural sciences (physics, chemistry, biology, and the like) and the axiomatic sciences (mathematics and statistics). Inductively-derived descriptive models map observations of physical processes into mathematical descriptions that can be treated as axioms (e.g., the various laws of physics). A synthetic model combines descriptive models of several physical processes with a structural model (representing the interactions of those processes) for the purpose of deducing or predicting the consequences of interactions. When applied together with elementary thermodynamic principles, circuit theory provides an excellent framework for synthetic modeling.

*Key words:* Network thermodynamics; Circuit modeling; Transducers

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## 1. Introduction

Being interested in signal processing carried out by the ear, in both hearing and vestibular senses, my student colleagues and I are constantly faced with physical systems that combine fluid mechanics, rigid-body mechanics, electrical process, diffusional processes, and chemical processes. For us, network thermodynamics (especially in the form of circuit theory) has proved to be a powerful tool for dealing with this mix of physical phenomena. Hoping that colleagues and students elsewhere

will find the tool as useful as we have, especially now that recently available CAD packages provide computer implementation of the analytical side of circuit theory, I offer this paper as a brief tutorial review of the subject. Most of it covers well-established material (some presented with a new perspective), including ideas published by three pioneers in network thermodynamics, Aharon Katchalsky, George Oster, and Alan Perelson, all of whom have been at Berkeley and have been colleagues and friends of Professor Bremermann.

## 2. Physical realms

Network theory is applicable to idealized physical processes in which some sort of entity, which I shall call stuff, flows or moves in some way and has been identified as being conserved. Such processes make up the basic analytic models in many

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Among the biophysics and bioengineering students at Berkeley as well as the students in the joint UC Berkeley–UC San Francisco Graduate Group in Bioengineering, Hans Bremermann is renowned and loved for his patient, clear teaching style — through which he has brought the concepts of biomathematics to life. This paper is offered as a token of my admiration for that side Professor Bremermann's career.

of the traditional subject areas of biophysics and biomathematics. For each kind of conserved stuff, one can identify a distinct physical realm. Thus, one can identify a hydraulic realm, in which water flows from place to place and is conserved as it does so; a pneumatic realm, in which air flows from place to place and is conserved; a particle diffusion realm, in which a particular species of dissolved particles moves from place to place and is conserved, and so forth.

The choice of the identity of the stuff presumed to be conserved and the measure of the amount of that stuff represented in a network model depend not only on the physical realm being modeled, but also on ease of model manipulation and on tradition. Conservation of mass is common to models in several realms, yet that conservation traditionally is represented differently in the various realms. For example, for continuum mechanics of solids, for nearly incompressible fluids and for compressible fluids under negligible variation in density, there is a tradition of using volume as a measure of mass. For diffusion of particles, there is a tradition of using the number of particles (often counted in moles) as a measure of mass. In rigid-body mechanics, there is a tradition of taking the shapes of rigid mass elements as being conserved, with translational and rotational displacements taken to be the measures. In the electric realm, charge traditionally is taken to be the conserved stuff. In the thermal and optical realms, thermal or optical energy often are taken to be the conserved stuffs. When those realms are coupled to others through certain (reversible, passive) transducers, the thermal or optical energy is not conserved; entropy is, however, and there is a tradition of treating entropy as the conserved stuff that flows (Yourgrau et al., 1982).

### 3. Advantages of network theory

Network theory provides a unified set of analytic and synthetic tools that can be applied to all of the realms. It is especially useful when the processes in those realms are highly interactive. The analytical side of network theory, now automated with available computational packages such as SPICE (Quarles, 1989), allows one to

deduce the dynamic behavior expected from a set of interacting physical processes whose parameters are known, or from a hypothetical set of interacting processes whose parameters are suspected. For example, one might use network analysis to deduce the effectiveness of a particular cardiac catheter in transmitting pressure from the aortic arch to a transducer outside the body. On its synthetic side, network theory allows one to establish bounds on the dynamic behavior achievable with various sets of interacting processes (regardless of how the individual processes are connected to one another). In other words, when one is attempting to design a particular device or system with a given set of elements, network theory can be used to determine what is possible and what is not. This side of network theory is especially powerful for dealing with physical processes that are behaving linearly or nearly linearly, and not very powerful for dealing with strongly non-linear processes. If one has data regarding the dynamic behavior of an existing device or system, the synthetic side of network theory can be used to translate those data into bounds on the underlying physical processes and their interactions.

### 4. Definition of network model

For the purposes of this paper, a network model is defined to be a collection of discrete (lumped) locales or states (e.g., chemical states) in which identified kinds of conserved stuff (fluid, charge, chemical reactants, particles, etc.) can accumulate, and a set of lumped paths connecting neighboring states or locales. Two lumped states or locales are considered to be neighbors if the stuff in question can flow directly from one of them to the other without passing through a third. The lumped paths provide the routes over which that flow can occur. The stuff is considered to be conserved if it is neither created nor destroyed in any of the states or locales or in any of the paths. Furthermore, although the stuff is allowed to accumulate at the various lumped states or locales, it is not allowed to accumulate in the lumped paths. For example, if two large reservoirs for water were connected by a pipe, one might construct a model in which each reservoir is repre-

sented as a single lumped locale and the pipe is represented as a single lumped path. In that case, the implied assumption is that all accumulation of water takes place in the reservoirs (the accumulation of water in the pipe is ignored); and all flow of water takes place through the pipe (flow of water in the reservoirs is ignored). Often in real systems, the same physical locale will serve conspicuously as both reservoir and flow path. A volume of matter, for example, could serve both as a reservoir for heat and as a path for heat flow to neighboring volumes. In that case, one might construct a model in which the volume in question is represented as a single lumped locale (for bookkeeping storage of heat) and one or more lumped paths (for bookkeeping heat flow). In network models, the process of accumulation and the process of flow always are depicted separately — even though they are intermingled in the volume being modeled.

A major advantage of network models is the fact that one can display them graphically, which, for many people is a great aid to intuition. The graphical representations that conventionally are used for network models include bond graphs, signal flow graphs, compartmental models and circuit models (Gardner and Barnes, 1942; Mason, 1956; Atkins, 1969; Desoer and Kuh, 1969; Karnop and Rosenberg, 1975; Chua et al., 1987; Thoma, 1990). In this paper I focus on circuit models.

## 5. Nodes and branches

A circuit model can be considered a graph comprising a set of nodes connected by a set of branches (Fig. 1). Among other things, nodes provide graphical devices for bookkeeping conservation of flowing stuff. Stuff is not allowed to accumulate at nodes, this leads to the following (node) rule:

The sum of the flows into each node at all times is instantly equal to the sum of the flows out of that node.

In general, one node (designated as the reference node) is not subject to this rule. This node represents a reference or ground state (or locale), and in circuit models applied to most physical realms

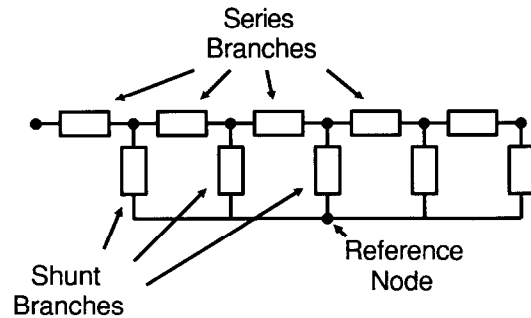


Fig. 1. A circuit graph, comprising nodes and branches.

it is treated as an inexhaustible source or sink for the conserved stuff. Each of the other lumped states or locales in the model is assigned a unique node and is represented by a branch connected directly from that node to the reference node. A branch with one end connected to the reference node is defined to be in a shunt configuration. Each lumped path in the model is represented by a branch connected directly between the two nodes assigned to the neighboring lumped states considered to be linked by the path. A branch connected between two nodes other than the reference node is defined to be in series configuration. Two branches are defined to be connected in series with one another if one end of each of them is connected to the same node, and no other branches are connected to that node.

Circuit theory traditionally involves two sets of variables: a set  $\{J_n\}$  of flow variables (where  $J_n$  is the model's representation of the flow of conserved stuff through branch  $n$ ) and a set  $\{F_n\}$  of efforts or potentials (where  $F_n$  is the model's representation of the tendency for stuff to flow spontaneously through branch  $n$ ). The potential or effort for each branch is said to be conjugate to the flow for that branch, and vice versa ( $J_n$  and  $F_n$  are conjugates to one another); variables associated with different branches (e.g.,  $J_n$  and  $F_m$ ) are non-conjugates to one another. If branch  $n$  connects nodes  $i$  and  $j$ , then  $J_n$  and  $F_n$  also could be labeled as  $J_{ij}(n)$  and  $F_{ij}$ , respectively, where  $J_{ij}(n)$  is the model's representation of the flow from node  $i$  to node  $j$  through branch  $n$ , and  $F_{ij}$  is the model's representation of the tendency for conserved stuff to flow spontaneously from node  $i$  to

node  $j$ .  $F_{ij}$  may be positive (representing tendency for stuff to flow spontaneously from  $i$  to  $j$ ) or negative (representing tendency for stuff to flow in the opposite direction); and  $J_{ij}(n)$  may be positive (representing stuff flowing from  $i$  to  $j$ ) or negative (representing stuff flowing in the opposite direction). Defined in this way,  $F_{ij}$  and  $J_{ij}(n)$  are said to have associated reference directions. In circuit models,  $F_{ij}$  and  $J_{ij}(n)$  are taken to be unique in the sense that at any instant  $F_{ij}$  has the same sign and magnitude for all branches connected between nodes  $i$  and  $j$ , and at any instant  $J_{ij}(n)$  has the same sign and magnitude throughout branch  $n$ .

The strict separation of flow (restricted to lumped paths) and accumulation (restricted to lumped states or locales) in network models is represented explicitly in circuit models by this uniqueness of  $J_{ij}(n)$ . The lumping of a path in a network model implies that the flow into one end of the path is taken instantly to emerge as the flow out of the other end; none is left behind to accumulate within the path. When a modeler considers whether or not to represent a real structure, such as a pipe carrying water between two reservoirs, as a lumped path, the decision ultimately must be based on the extent to which the structure exhibits a unique flow. For candidate paths that do not leak, the decision will depend on two things: (1) the rate at which steady state flow is established through the real candidate path, and (2) the meaning of ‘instantly’ in the situation at hand. Item (1) depends on the physics involved in the flow process and on what is connected to the two ends of the candidate lumped path. Item (2) depends on the temporal resolution that one demands in the deductions to be drawn from the network model, and that in turn depends on the purpose for which the model is constructed. Problems arise because any real path that is a candidate for treatment as a lumped path in a network model will be capable of accumulating a finite quantity of conserved stuff, leading to temporary deviations from the unique-flow property whenever the potential or effort across the path is changed. When steady state flow is not established in a real path in times that are short in comparison with the temporal resolution desired in the

deductions, then the standard remedy is to represent that path as a cascade of lumped locales connected by lumped paths. For a real path through which flow is diffusion-like, temporal resolution in the deductions usually increases as the square of the number of lumped locales in the model of the path.

As it has been described so far in this brief review, the circuit model has two variables associated with each branch, a flow  $J_n$  through it and an effort or potential  $F_n$  across it. In that case flow is called the through variable and effort or potential the cross variable. Circuit models also may be constructed with effort or potential as the through variable and flow as the cross variable. A pair of circuit models that represent precisely the same physical relationships, thus leading to precisely the same dynamic equations, employing these two different bases are said to be duals of one another. In the translational and rotational realms of rigid-body mechanics, circuit models traditionally are based on potential (force or torque) being the through variable and flow (translational or rotational velocity) the cross variable. For other physical realms, circuit models usually conform well to physical intuition when they are based on flow being the through variable, effort or potential the cross variable. If one envisions each rigid mass element as a path (with inertia) along which uniform velocity (unique flow) is established instantly, then the same form of circuit model (rather than its dual) will conform to physical intuition in rigid body mechanics as well.

## 6. Potentials and free energy

There are at least two ways to define the variable,  $F_{ij}$ . The traditional approach has been to invoke the linear empirical laws of non-equilibrium thermodynamics (e.g., see Daniels and Alberty, 1955; Kittel, 1958; Fox and McDonald, 1978; Yourgrau et al., 1982): Fourier’s law, which states that the heat flow along a thermal conduction path is directly proportional to the temperature difference between the two locales connected by the path; Fick’s law, which states that the diffusional flow of particles along a path is directly proportional to the difference in particle

concentration at the two locales connected by the path; Poiseuille's equation, which states that the (fully-developed, laminar) flow of a Newtonian fluid through a horizontal pipe is directly proportional to the pressure difference between the two locales connected by the pipe; Ohm's law, which states that the charge flow along a path is directly proportional to the voltage difference between the two locales connected by the path; and so forth. The variables associated with the flows are temperature, concentration, pressure, voltage, and so forth. These are not always linear measures of potential, in the thermodynamic sense, and therefore often are categorized as efforts (e.g., see Thoma, 1990).

The alternative approach is derived from the thermodynamic definition of potential. If stuff tends to flow spontaneously and predictably from locale  $i$  to locale  $j$ , and if one could harness that flow appropriately, it could be made to do work. The reason for including 'predictably' in this statement is the principle that work cannot be obtained from the random motions associated with thermal energy under conditions of thermal equilibrium. Taking the thermodynamic approach to circuit theory, one defines  $F_{ij}$  to be the maximum possible work available to the observer when a unit quantity of stuff moves from state or locale  $i$  to state or locale  $j$ .  $F_{ij}$  specifically excludes the pressure–volume work that must be done against the atmosphere in order for the stuff to move (that component of work is not available to the observer).

With this exclusion,  $F_{ij}$  by definition is the change in the Gibbs free energy ( $G$ ) that takes place in the model when a unit quantity of stuff moves from state  $j$  to state  $i$ :

$$F_{ij} = \frac{\delta G}{\delta Q_i} - \frac{\delta G}{\delta Q_j} \quad (1)$$

where  $Q_i$  and  $Q_j$  are the total quantities of stuff stored in states  $i$  and  $j$ , respectively. Thus, a positive value of the potential  $F_{ij}$  implies free energy increase when stuff is moved from state  $j$  to state  $i$ , and the availability of work to the observer when the stuff returns again to state  $j$ . In circuit models based on this definition of  $F_{ij}$ , it is easy to evaluate the flow of free energy. For that

reason, such circuits are especially useful for carrying out analysis and design involving transducers, through which free energy (but not conserved stuff) can flow from one physical realm to another.

Following the tradition of nineteenth century thermodynamics, one can derive the forms of the potentials for the various physical realms by a series of thought experiments in which ideal transducers harness the flow of conserved stuff in each realm and convert it to force-times-distance ( $f \times d$ ) work in the translational, rigid-body mechanical realm. The Carnot engine is an example of such a transducer. In that case the conserved flow of entropy between two thermal reservoirs is harnessed to do  $f \times d$  work. If the imagined transducer produces the maximum mechanical work possible for the amount of conserved stuff transferred between two states (e.g., the transduction process is imagined to be carried out so slowly that none of the potential for work is lost through friction), if the potential difference ( $F_{ij}$ ) between the two states or locales is imagined to remain constant throughout the transduction process, and if any component of the  $f \times d$  work that must be done against the atmosphere is excluded, then the remaining  $f \times d$  work divided by the total amount of conserved stuff transferred from state or locale  $i$  to state or locale  $j$  is defined to be  $F_{ij}$ .

When the potential is a log function (see Table 1), it represents potential to extract heat from the thermal realm and convert it to work (i.e., by virtue of an increase in entropy in the physical realm for which the potential is being derived). For the (ideal) pneumatic realm, the expression for  $F_{ij}$  can be deduced by invoking the ideal gas law and employing an imaginary transducer (e.g., involving a piston) that uses pressure difference to generate  $f \times d$  work as 1.0 kg of gas particles is transferred from a reservoir at pressure  $P_i$  to a reservoir at pressure  $P_j$  (e.g., see Fox and McDonald, 1978). For the (ideal) diffusional realm,  $F_{ij}$  can be deduced by invoking the Pfeffer–van't Hoff law and employing an imaginary transducer that uses osmotic pressure to generate  $f \times d$  work as 1.0 kg of particles is transferred from a reservoir at concentration  $c_i$  to a reservoir at concentration  $c_j$ .

Table 1  
Examples of conjugate potentials and flows in various physical realms

Physical realm	Conserved stuff (SI unit)	Flow (SI unit)	Traditional effort (SI unit)	Potential ( $F_i - F_o$ ) (joule/unit stuff)
Chemical	Number of particles mol	Reaction rate mol/s	Chemical potential ( $\mu$ ) J/mol	$\mu_i - \mu_o$
Continuum mechanical	Volume $m^3$	Volume flow $m^3/s$	Stress ( $\sigma$ ) $N/m^2$ ( $J/m^3$ )	$\sigma_i - \sigma_o$
Electric	Charge C	Charge flow A (C/s)	Electric potential ( $V$ ) V (J/C)	$V_i - V_o$
Hydraulic (horizontal flow)	Volume $m^3$	Volume flow $m^3/s$	Pressure ( $p$ ) Pa ( $J/m^3$ )	$p_i - p_o$
Optical (black-body radiator)	Radiant energy J	Energy flux W	Temperature ( $T$ ) K	$\log_e (T_i/T_o)$ $\approx (1/T_o)(T_i - T_o)$
Particle diffusion (ideal)	Number of particles mol	Diffusion rate mol/s	Concentration ( $c$ ) $mol/m^3$	$RT \log_e (c_i/c_o)$ $\approx (RT/c_o) (c_i - c_o)$
Particle diffusion (non-ideal)	Number of particles mol	Diffusion rate mol/s	Concentration ( $c$ ) $mol/m^3$	$(RT) \log_e(a_i/a_o)$ ( $a$ = activity)
Pneumatic (ideal gas)	Mass kg	Mass flow kg/s	Pressure ( $p$ ) Pa	$(1000 RT/M) \log_e(p_i/p_o)$ $\approx (1000 RT/Mp_o) (p_i - p_o)$
Pneumatic (non-ideal gas)	Mass kg	Mass flow kg/s	Pressure ( $p$ ) Pa	$(1000 RT/M) \log_e(f_i/f_o)$ ( $f$ = fugacity)
Rigid Body (translational motion along one horizontal axis)	Shape m	Velocity m/s	Force ( $F$ ) N (J/m)	$F_i - F_o$
Rigid Body (rotational motion about one vertical axis)	Shape rad	Rotational velocity rad/s	Torque ( $T$ ) Nm (J/rad)	$T_i - T_o$
Thermal	Thermal energy J	Heat flow W	Temperature ( $T$ ) K	$\log_e (T_i/T_o)$ $\approx (1/T_o) (T_i - T_o)$
Thermal	Entropy J/K	Entropy flux W/K	Temperature ( $T$ ) K (J per J/K)	$T_i - T_o$

$R$  = gas constant = 8.317 J/mol K;  $M$  = gram molecular weight of stuff.

For a (conserved) flow of heat from a reservoir at temperature  $T_i$  to one at  $T_j$ , imagine that the process is carried out in small temperature steps through a sequence of intervening reservoirs (each with a slightly lower temperature than the previous one), with a separate Carnot engine doing the transduction at each step. Each Carnot engine actually converts a fraction of the flowing heat to work. In the process being imagined here, the flowing heat is taken to be conserved. This can be

accomplished by replacing the heat converted to work at each step with heat from the thermal realm (i.e., each transduction step will begin with the same amount of heat being drawn from the hotter reservoir). Thus, the conserved, multistep transfer of heat from the hottest reservoir in the sequence (at  $T_i$ ) to the coolest (at  $T_j$ ) is taken to produce a second transfer of heat, all of which is converted to work. The logarithmic relationship between converted heat and  $T_i/T_j$  arises when one

assumes that the temperature steps become infinitesimal and the number of steps infinite.

An axiom of circuit theory is additivity of effort or potential:  $F_{ao} - F_{io} = F_{ab} + F_{bc} + \dots + F_{gh} + F_{hi}$ , where this relationship holds for all possible routes between nodes  $a$  and  $i$ . Experience tells us that this relationship holds for the variables (e.g., pressure, concentration, temperature and voltage) usually employed as measures of effort. If that is true, then it also will apply to potentials that are logarithmically related to the ratios of those efforts (as in Table 1). For potentials defined as they are in Table 1, this axiom translates to a statement of uniqueness of free energy: The change in free energy when any amount of stuff is transferred from one lumped state or locale to another is taken to be independent of the route used in the transfer.

There also is a temporal aspect to the uniqueness of free energy. The terms on the right hand side of Eq. 1, and therefore the potential, are well defined only if we impose the following rule: the free energy change associated with the transfer of stuff from one lumped state to another is independent of the time elapsed since the transfer took place (as long as the stuff remains in the new locale). In other words, when a unit of stuff is represented as being transferred from state or locale  $j$  to state or locale  $i$ , the free energy in the network model is assumed instantly to change to the (unique) value corresponding to the new distribution of stuff. When finite volumes (or hypervolumes) in state space or physical space are represented as lumped states or locales, then the validity of this axiom is based on the assumption that all of the stuff within each volume is distributed (e.g., spatially and energetically) in a steady state fashion at all times (i.e., whenever stuff flows in or out of the volume, the distribution of that stuff instantly relaxes to steady state). This assumption is a good one if relaxation takes place in times that are short in comparison with the temporal resolution desired in the deductions from the circuit model. The time required for relaxation to within an acceptable proximity of steady state normally decreases as the size of the volume or hypervolume decreases. As greater temporal res-

olution is demanded in the modeling deductions, one usually must increase the number of lumped states or locales in the circuit model and let each one represent a smaller volume in physical space or a smaller volume or hypervolume in state space.

The operations of many biological structures (such as neurons and muscle cells) as well as the operations of biophysical measuring devices (such as electrodes and electrophoresis equipment) are based on flows of charged particles (ions) in fluids. If the fluid itself is not moving, then the particle will move as a consequence of its random thermal motion (diffusion), as a consequence of electric fields acting on it, as a consequence of chemical reactions in which it is involved, and as a consequence of gravity. For particles (such as inorganic ions) with low mass, the effects of gravity usually are ignored. They become important, however, in some devices used to sort and sense large biological molecules. The effects of gravity also are important in hydraulics when vertical flow in a gravity field is involved, and in many instances of rigid-body and continuum mechanics of solids in a gravity field. Therefore, the biophysicist and biomathematician often must deal with situations in which more than one physical phenomenon contributes to the total potential for some stuff. If the contributed components of potential are defined in such a way that they all refer to the same measure of particle quantity (e.g., all given as free energy per kilogram of the particle species in question), then they can be summed: e.g.,  $F_{ij}(total) = F_{ij}(diffusion) + F_{ij}(electric) + F_{ij}(chemical) + F_{ij}(gravity)$ . With mass as the conserved stuff and 1 kg as the unit measure of that stuff, a linearized version of this expression for a uniform gravitational field would be  $F_{ij}(total) = (1000RT/Mc_0)(c_i - c_j) + (1000zF/M)(V_i - V_j) + (1000/M)(\mu_i - \mu_j) + g(h_i - h_j)$ , where  $c_0$  is the reference (ground) concentration level defined for the particle species in question,  $z$  is the ionic valence of the particle,  $F$  is the Faraday constant,  $g$  is the equivalent acceleration of gravity, and  $h$  is vertical height. In hydraulics, with volume as the measure of stuff and the possibility of vertical flow,  $F_{ij}(total) = P_i - P_j + \rho g(h_i - h_j)$  is the potential, where  $\rho$  is the density of the fluid.

## 7. Free energy flow

When potential is defined as free energy per unit of conserved stuff, then the product of (conjugate) potential and flow for a given branch in a circuit model is equal to the rate at which free energy is represented as flowing between that branch and the rest of the circuit. When associated reference directions are used and the product is positive, the free energy flow is represented as being into the branch. Thus, free energy is depicted as flowing from branch to branch, in which case energy conservation is represented by requiring that, at each instant, the sum of the flows of free energy into all ( $N$ ) branches is zero:

$$\sum_{n=1}^N F_{ij} J_{ij}(n) = 0 \quad (2)$$

Although it represents the first law of thermodynamics when  $F_{ij}$  is free energy per unit of conserved stuff, Eq. 2 is asserted by Tellegen's theorem to be more general (Desoer and Kuh, 1969). According to Tellegen's theorem, Eq. 2 is true for any set of potential or effort values that conform to the additivity rule taken together with any set of flow values (for the same graph) that conform to the node rule.

## 8. Constitutive relationships

Whether or not the product  $FJ$  has the dimensions of power, each branch in a circuit model explicitly represents a specific relationship between  $F$  and  $J$ . By convention, these relationships usually are separated into five categories: (1) resistive relationships, in which the present instantaneous value of  $F_n$  is uniquely determined by the present instantaneous value of  $J_n$ , and vice versa; (2) capacitive relationships, in which the present instantaneous value of  $dF_n/dt$  is uniquely determined by that of  $J_n$ , and vice versa; (3) inertial relationships, in which the present instantaneous value of  $dJ_n/dt$  is uniquely determined by that of  $F_n$ , and vice versa; (4) flow sources, each of which produces a flow,  $J_n$ , that is independent of  $F_n$ ; and (5) potential or effort sources, each of which produces a potential or effort,  $F_n$ , that is independent of  $J_n$ .

If one assumes that the change in free energy is instantly and uniquely defined when a quantity,  $\delta Q$ , of conserved stuff is transferred from state  $j$  to state  $i$ , then  $\delta G/\delta Q_i$  and  $\delta G/\delta Q_j$  in Eq. 1 are well defined, as will be the capacitive relationship

$$\frac{dF_{ij}}{dt} = \left( \frac{\delta^2 G}{\delta Q_i^2} - \frac{\delta^2 G}{\delta Q_j^2} \right) \frac{dQ}{dt} \quad (3)$$

where  $dQ/dt$  is the rate at which stuff is transferred from state  $j$  to state  $i$ . Because  $Q_i$  and  $Q_j$  may change independently, their bookkeeping usually is separated in a circuit model:

$$F_{ij} = F_{io} - F_{jo}$$

$$\frac{dF_{io}}{dt} = \left( \frac{\delta^2 G}{\delta Q_i^2} - \frac{\delta^2 G}{\delta Q_o^2} \right) \frac{dQ_i}{dt} \quad (4)$$

$$\frac{dF_{jo}}{dt} = \left( \frac{\delta^2 G}{\delta Q_j^2} - \frac{\delta^2 G}{\delta Q_o^2} \right) \frac{dQ_j}{dt}$$

Thus, the reference state can be envisioned as an intermediate destination when stuff is transferred from state  $j$  to  $i$ . In a circuit model,  $dQ_i/dt$  is represented as flow of stuff into the shunt branch representing state  $i$ . In the case of the shunt branch representing a capacitive relationship such as either of those in Eq. 4, the modeler may envision the flow of conserved stuff to take place at one end of the branch only — the end not connected to the reference node. In effect, the shunt capacitive branch represents a reservoir. A flow of stuff in and out of one end conforms to one's physical intuition about accumulation of stuff in reservoirs: when heat or fluid or particles flow in and out of one entrance to a reservoir there is no need for compensatory flow of the same stuff in or out of a second entrance. The potential or effort at the entrance to the reservoir, however, will be measured relative to a reference state (represented in the circuit model by the reference node). Connection of the one end of the capacitive shunt branch to the reference node serves as a graphical representation of that fact.

In at least three physical realms — electric, hydraulic and pneumatic — there are structures that can be modeled as capacitive branches in series configuration. The parallel plate electrical capacitor derives its large capacity for charge storage (i.e., its ability to accumulate large



amounts of charge without large, concomitant changes in electric potential) by storing charge in the form of compact dipole pairs: every positive charge stored on one plate is accompanied by a nearby negative charge on the other plate. A terminal is connected to each plate; and when charge flows onto one plate, the same amount of charge is displaced from the other plate, leaving the appropriate countercharge behind. The overall capacitor is left with no net charge. Charge has effectively been transferred, however, from one plate to the other; and the electric potential difference between the plates has been changed. To the extent that the displacement of charge occurs instantly, the parallel plate capacitor exhibits a unique flow and thus behaves in the same manner as a lumped path. Therefore, the (capacitive) branch representing the capacitor in a circuit model may be placed in series configuration. An elastic, deformable barrier, placed in the path of fluid flow is an analogous device. Fluid flowing into one side of the device deforms the elastic barrier, displacing the same amount of fluid from the other side and creating a change in the pressure difference from one side to the other. The cupula of the semicircular canal in a vertebrate inner ear is such a device, and it often is represented as a series capacitive branch in circuit models of the canal.

Some forms of flow, such as the flow of populations of charged particles, the flow of liquids, and the motions of solids, exhibit conspicuous momentum or apparent momentum; once the flow has started it tends to continue, and infinite potential would be required to halt the flow instantly. In circuit models, momentum of flow is represented in inertial branches. Capacitive branches and inertial branches normally account for stored free energy. Free energy stored in inertial elements is that associated with the motion of stuff — kinetic energy. That stored in capacitive branches is the free energy of accumulation of stuff — potential energy.

The second law of thermodynamics assures us that whenever stuff flows from one state or locale to another, a finite amount of free energy is dissipated. In circuit models, dissipation of free energy usually is represented by flow through a

resistive branch. A lumped path that exhibits both momentum and free energy dissipation conventionally is represented by a resistive branch connected in series with an inertial branch (representing one flow associated with two additive components of potential). The node shared by the two branches is assigned a potential that is not associated with a state or locale. Instead, it is a computational convenience.

A source variable (e.g., the potential associated with a potential source) may be independent of all other potentials and all flows in the circuit model, or it may depend on one or more potentials or flows other than its own conjugate flow or potential. Independent sources commonly are used to represent application of external stimuli or signals to the system being modeled. Dependent sources (e.g., branch  $n$ , connecting nodes  $i$  and  $j$ , with  $J_{ij}(n)$  being independent of  $F_{ij}$  but dependent on  $F_{ab}$ ) often are used in circuit representations of transducers. Dependence on non-conjugate variables can be extended to resistive branches, capacitive branches and inertial branches. In resistive branch  $n$  (connecting nodes  $i$  and  $j$ ), for example,  $J_{ij}(n)$  might be dependent not only on  $F_{ij}$ , but also on  $F_{ab}$  or on other potentials (or flows). Resistive branches of this sort are especially convenient in SPICE circuit models for representing non-linear biophysical interactions at the cellular level (e.g., those involving enzyme kinetics and those involving ion-channel gating).

When it is assigned its constitutive relationship, each branch in a circuit model becomes an element of that model. In the circuit graph, each element of this kind has two terminals, and the elements are connected to one another at the nodes. When it represents dynamics in two or more physical realms, with exchanges of free energy between the represented realms, the transducers in the circuit model often are depicted as two-port elements (Fig. 2). Each port of a two-port element corresponds to a single branch in the circuit model, and the graphical construction of the element (as a box with two ports) depicts coupling between those two branches. Alternatively, a transducer may be depicted as an appropriately connected set of two-terminal elements, in some of which the constitutive relationships in-

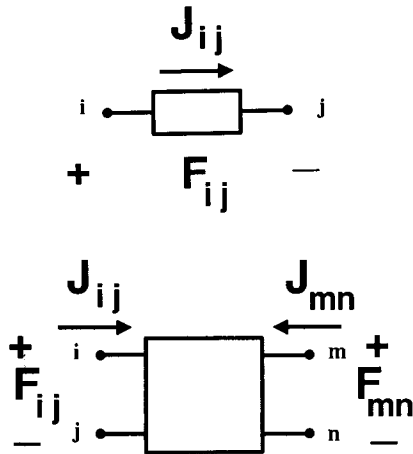


Fig. 2. A two-terminal element (top) and a two-port element (bottom). The + and - signs indicate the reference direction for  $F_{ij}$ . When  $F_{ij}$  is a positive number, stuff will tend to flow spontaneously from node  $i$  to node  $j$ . The arrow indicates the reference direction for  $J_{ij}$ ; when  $J_{ij}$  is positive, stuff flows from node  $i$  to node  $j$ . When the direction of the arrow for a flow is from + to - for the conjugate potential or effort, the reference directions are said to be associated.

clude dependence on non-conjugate potentials or flows. The latter configuration is well-suited to circuit modeling of transducers with SPICE, the former is useful for considering the properties of transducers as individual elements.

### 9. Passive and active elements

Usually a circuit model comprises a set of connected elements that represent local accumulation or dissipation of free energy that already has entered the circuit as a whole, plus one or more elements that represent processes by which free energy enters the circuit from elsewhere. The former are said to be passive elements, the latter are active elements. The role played by a given element can be ascertained from its constitutive relationships. For a passive two-terminal element (i.e., one that is capable only of accumulating or dissipating free energy) the constitutive relationship must be such that the inequality

$$\int_{\tau_0}^t F_{ij}(t)J_{ij}(t) dt + E_0 \geq 0 \quad (5)$$

will be true for all initial time  $\tau_0$ , for all time

$\tau \geq \tau_0$ , and for all possible functions  $J_{ij}(t)$  or  $F_{ij}(t)$ , whichever is taken to be the input,  $E_0$  being the free energy stored in the element at time  $t = \tau_0$  (see Desoer and Kuh, 1969, p. 802). If this condition is not met, the element is active.

The corresponding inequality for a passive two-port element is

$$\int_{\tau_0}^t F_{ij}(t)J_{ij}(t) dt + \int_{\tau_0}^t F_{mn}(t)J_{mn}(t) dt + E_0 \geq 0 \quad (6)$$

Thus, viewed separately as a two-terminal element, an individual port of a two-port need not meet Ineq. 5 in order for the two-port element, as a whole, to be passive. This leads to ambiguity with respect to models of transducers. To a modeler considering two physical realms connected by a transducer, the transducer would translate into a passive two-port if it simply passed free energy between the realms. To a modeler considering only one of those realms, the same transducer would translate into an active two-terminal element, bringing free energy into the circuit from outside. Thus, an electromagnetic transducer could be an active two-terminal motor to a mechanical engineer, an active two-terminal generator to an electrical engineer, or a passive two-port element to a transducer engineer. Thus, the definitions of passive and active are based on the boundaries assigned to the system being modeled.

### 10. Linear, time invariant circuits

The discussion to this point has not been limited with respect to the classes of constitutive relationships assigned to the circuit elements. With SPICE and other software packages for circuit modeling, circuit models with wide varieties of non-linear constitutive relationships can be analyzed easily, and there are graphical methods that aid one's intuition about the dynamic behaviors (such as limit cycles) of such circuits. On the other hand, considerable effort has been focussed on the special class of circuit models known as linear and time-invariant. Because such models are good representations of a wide variety of biophysical phenomena, and because formal studies of such models have left us a rich heritage of very useful concepts and tools for thinking

about them, I devote the rest of this review to them.

A linear, time-invariant circuit model is one in which the constitutive relationship of each branch can be written as a time-invariant, linear functional of one or more potentials or flows in the circuit model. For branches representing relationships between conjugate variables only, time-invariant linear functionals include the following:

$$F_{ij} = R_{ij} J_{ij} \quad F_i = \frac{1}{C_{ij}} \int_{-\infty}^t J_{ij} dt \quad F_{ij} = I_{ij} \frac{dJ_{ij}}{dt} \quad (7)$$

where  $R_{ij}$ ,  $C_{ij}$  and  $I_{ij}$  are constant, real numbers, usually called resistance, capacitance and inductance, respectively. The relationships of Eq. 7 represent passive processes only if the resistances, capacitances and inductances are not negative. The only independent sources that meet the (additivity and homogeneity) requirements for linearity are the trivial ones,  $F = 0$  and  $J = 0$ . Non-trivial independent sources are non-linear circuit elements and thus are excluded from linear circuit models. The linear two-terminal constitutive relationships imply no direction of causality, neither  $F_{ij}$  nor  $J_{ij}$  is taken to be cause or effect or to be the dependent variable or the independent variable.

## 11. Impedances and admittances

In single-input, single-output analysis of a circuit model, the goal often is to find a general relationship between a designated independent source variable and a designated response variable. In zero-state or sinusoidal steady-state analysis of linear networks, that relationship can be stated in the form of an impedance, an admittance, or a dimensionless transfer ratio (e.g., see Desoer and Kuh, 1969). The concepts of impedance, admittance and transfer ratio arise from the use of Laplace transforms in zero-state analysis and from the use of phasor transforms (or single-sided Fourier transforms) in sinusoidal steady-state analysis. Suppose, for example, that the designated source variable is the flow,  $J_{ij}(t)$ , through an independent flow source connected between nodes  $i$  and  $j$ . If the designated response were the resulting potential between nodes  $i$  and  $j$ , one could describe the relationship as follows:

$$F_{ij} = Z_{dp} J_{ij} \quad (8)$$

where  $Z_{dp}$  is a driving-point impedance;  $J_{ij}$  is the Laplace or phasor transform of  $J_{ij}(t)$ ; and  $F_{ij}$  is the Laplace or phasor transform of  $F_{ij}(t)$ . If the designated source variable had been the potential,  $F_{ij}(t)$  of an independent potential source connected between nodes  $i$  and  $j$ ; and the designated response had been the flow through that source (from node  $i$  to node  $j$ ), the relationship might have been described as

$$J_{ij} = Y_{dp} F_{ij} \quad (9)$$

where  $Y_{dp}$  is a driving-point admittance. Because they were obtained for the same pair of nodes, the driving-point impedance and driving-point admittance in this case are reciprocals of one another. Thus, a driving-point impedance or admittance bears no implication regarding causality — it relates potential to flow but does not imply that one is cause, one effect. Given as phasor transforms, the driving-point impedances for the three basic linear two-terminal elements are

$$Z_{ij} = R_{ij} \quad Z_{ij} = \frac{1}{i\omega C_{ij}} \quad Z_{ij} = i\omega I_{ij} \quad i = \sqrt{-1} \quad (10)$$

Transfer relationships, on the other hand, always imply a direction of causality. If the designated source were  $F_{ij}$  and the designated response were  $F_{mn}$ , the generalized relationship would be:

$$F_{mn} = T_i F_{ij} \quad (11)$$

where  $T_i$  is a dimensionless transfer ratio. If the situation had been reversed, with  $F_{mn}$  as designated source and  $F_{ij}$  as designated response, the transfer ratio would not be  $1/T_i$  (it also would not, generally, be  $T_i$ ). The computation of  $T_i$  was based on  $F_{ij}$  being cause,  $F_{mn}$  being effect, and that is the only situation to which  $T_i$  can be expected to apply. The same thing is true of transfer admittances and transfer impedances

$$J_{mn} = Y_i F_{ij} \quad F_{mn} = Z_i J_{ij} \quad (12)$$

In general, the reciprocals of  $Y_i$  and  $Z_i$  have no meaning. By convention, the variable designated as cause in transfer relationships appears immediately to the right of the corresponding transfer ratio, admittance, or impedance.

In the process of formulating a rational basis for synthesis of analog filter circuits, electrical engineers and their colleagues from applied mathematics amassed a thorough knowledge of the properties of circuits synthesized with passive, linear elements. This knowledge often is expressed in terms of limitations on driving-point and transfer impedances and transfer ratios. As digital signal processing has replaced analog filter technology, this body of knowledge has been becoming increasingly esoteric for engineers. It stands, however, as a potentially rich resource for biophysicists and biomathematicians — e.g., as part of an epistemology for non-equilibrium thermodynamics. I refer the interested reader to the first three chapters of Guillemin (1957), and especially to Table 1 on p. 66 of that book.

## 12. Linear two-port elements

In contrast to those for two-terminal elements, two-port and multiport constitutive relationships are based on explicitly stated directions of causality (Linville and Gibbons, 1961; Desoer and Kuh, 1969). Each of the element's branches has two variables (a potential and a flow), making four variables for the two-port and  $2n$  variables for the  $n$ -port. For each set of constitutive relationships, half of the variables are selected as dependent variables, and half as independent variables. Thus, for the two-port there are six sets of constitutive relationships. If the constitutive relationships are linear, however, the modeler can derive all six sets from any one. To simplify the notation, each branch (port) is assigned a single, unique index, and each branch variable is assigned the single index of its branch. In Fig. 2, for example, let the branch between nodes  $i$  and  $j$  be port 1 and the branch between nodes  $m$  and  $n$  be port 2:

$$\begin{aligned} F_{ij} = F_1 \quad F_{mn} = F_2 \\ J_{ij} = J_1 \quad J_{mn} = J_2 \end{aligned} \quad (13)$$

Two commonly used sets of linear constitutive relationships are

$$\begin{bmatrix} F_1 \\ F_2 \end{bmatrix} = \begin{bmatrix} z_{11} & z_{12} \\ z_{21} & z_{22} \end{bmatrix} \cdot \begin{bmatrix} J_1 \\ J_2 \end{bmatrix}$$

$$\begin{bmatrix} F_1 \\ J_2 \end{bmatrix} = \begin{bmatrix} h_{11} & h_{12} \\ h_{21} & h_{22} \end{bmatrix} \cdot \begin{bmatrix} J_1 \\ F_2 \end{bmatrix} \quad (14)$$

Each parameter set is represented as a matrix that maps a vector comprising the two variables selected as independent into a vector comprising the two variables selected as dependent. Each parameter is an admittance, and impedance, or a transfer ratio. As such, it need not simply be a real constant. Thus,  $z_{11}$  is the driving-point impedance at port 1 when no flow is allowed to occur at port 2, and  $z_{12}$  is the transfer impedance relating the potential at port 1 to the flow into port 2 when no flow is allowed to occur at port 1. In spite of the explicit representation of causal direction, unlike the conventional black-box system element (in which input and output are completely isolated and the transfer relationship is taken to be independent of context), the two-port model embodies context dependence. This is its great advantage; it allows the modeler to incorporate context dependence (e.g., the impacts of source impedance and load impedance) in design and analysis.

For example, when a two-terminal load impedance  $Z_L$ , is connected across port 2, the driving-point impedance at port 1 is easily found to be

$$Z_{dp} = z_{11} - \frac{z_{12}z_{21}}{z_{22} + Z_L} = h_{11} - \frac{h_{12}h_{21}}{h_{22} + 1/Z_L} \quad (15)$$

When phasor notation is employed (for sinusoidal steady-state conditions), passivity requires that the real part of any impedance not be negative. For  $Z_L$  with non-negative real part,  $Z_{dp}$  also must have a non-negative real part. Therefore, conditions that must be met by a two-port element in order for it to be passive include

$$\operatorname{Re} \left\{ h_{11} - \frac{h_{12}h_{21}}{h_{22}} \right\} \geq 0 \quad (16)$$

$$\operatorname{Re} \left\{ z_{11} - \frac{z_{12}z_{21}}{z_{22}} \right\} \geq 0 \quad (17)$$

For modeling with SPICE or other purposes, translation of a linear, time invariant two-port element into an equivalent circuit comprising two-

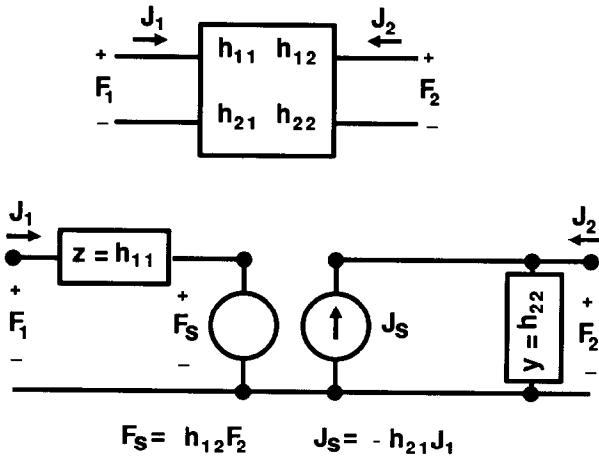


Fig. 3. Alternative representations of a two-port element, based on the  $h$  parameters.

terminal elements (Fig. 3) can be accomplished easily by application of the Thévenin–Norton theorem (e.g., see Chua et al., 1987, p. 251).

### 13. Linear transducers

People design and use transducers for three purposes: (1) to convert free energy from one physical realm into a generally usable form in another physical realm, (2) to convert free energy into purposeful action, and (3) to convert free energy into a form in which the information it contains can be processed easily. Transducers used for purpose (1) sometimes are called generators, those used for purpose (2) are actuators and those used for purpose (3) are sensors. Occasionally, actuators and sensors are idealized as being able to transfer free energy between two physical realms, but not being able (by themselves) to store or dissipate free energy. In terms of the  $z$  and  $h$  parameters, the constitutive relationships of the two-port models for linear versions of such ideal transducers are

$$\begin{bmatrix} F_1 \\ F_2 \end{bmatrix} = \begin{bmatrix} 0 & z_{12} \\ z_{21} & 0 \end{bmatrix} \cdot \begin{bmatrix} J_1 \\ J_2 \end{bmatrix} \quad (18)$$

$$\begin{bmatrix} F_1 \\ J_2 \end{bmatrix} = \begin{bmatrix} 0 & h_{12} \\ h_{21} & 0 \end{bmatrix} \cdot \begin{bmatrix} J_1 \\ F_2 \end{bmatrix}$$

According to the Onsager reciprocity theorem for passive linear transducers involving microscopic reversibility (Onsager, 1931a, b),

$$z_{12} = z_{21} \quad h_{12} = -h_{21} \quad (19)$$

Combining this with the conditions for passivity based on driving-point impedance, one has the following constraints on the transfer impedance ( $z_{12}$ ) and transfer ratio ( $h_{12}$ ) of the ideal linear, passive, reciprocal transducer of Eq. 18:

$$\text{Re}\{z_{12}^2\} \leq 0 \quad \text{Re}\{h_{12}^2\} \geq 0 \quad (20)$$

Real transducers that are modeled well as passive, reciprocal two-ports include pistons and diaphragms (between hydraulic or pneumatic realms and translational rigid-body mechanical realm), pulleys, semilevers and rack-and-pinion gears (between rotational rigid-body mechanical realm and translational rigid-body mechanical realm), and Seebeck–Peltier devices (between electric and thermal realms). A two-port model of an ideal (e.g., massless, frictionless) version of such a device can take the following form:

$$\begin{aligned} h_{11} &= 0 & h_{12} &= \lambda_t \\ h_{21} &= -\lambda_t & h_{22} &= 0 \end{aligned} \quad (21)$$

Wire coils (transducers between electric and magnetic realms) and electromagnetic velocity transducers (between electric and mechanical realms) are passive but antireciprocal (e.g., see Merhaut, 1981). In fact, for any transducer based on flow-dependent potential sources (i.e., real transfer impedances) and in which the self impedances ( $z_{11}$  and  $z_{22}$ ) can be made arbitrarily small (which is true, for example, of geophones, electromagnetic loudspeakers, electromagnetic motor/generators, and other electromagnetic velocity transducers), Eqs. 15 and 17 imply that reciprocity is inconsistent with passivity. Based on the fact that they involve rotational motion (e.g., of moving charge in a magnetic field), Onsager (1931a, b) excluded such devices from his reciprocity theorem. A two-port model of ideal versions of these antireciprocal transducers takes the following form:

$$\begin{aligned} z_{11} &= 0 & z_{12} &= r_t \\ z_{21} &= -r_t & z_{22} &= 0 \end{aligned} \quad (22)$$

Both two-port models (Eqs. 21 and 22) translate passive resistors connected across port 2 into positive real driving-point impedances at port 1 (see Eq. 15). Flow through port 1 thus is dissipative; free energy is represented as being lost from the circuit connected to that port. With these ideal models, however, all of that free energy is represented as being transferred to the resistor connected across port 2. The two-terminal resistor itself can be considered to be a transducer, but one for which free energy is not tracked after it enters the device. With the reciprocal two-port model of Eq. 21, a capacitor across port 2 translates to a capacitive driving point impedance at port 1, and an inertial impedance across port 2 translates to an inertial driving-point impedance at port 1. The antireciprocal two-port of Eq. 22 does the opposite; it translates a capacitor across port 2 to an inertial driving-point impedance at port 1, and vice versa. The passive, antireciprocal two-port element represented by Eq. 22 is known as a gyrator (another device with antireciprocal properties is a gyroscope serving as a transducer between orthogonal translational rigid-body mechanical realms). Thus, a passive device (capacitor) that accumulates potential energy is converted, by a gyrator, into a passive device that appears to possess inertia and to accumulate kinetic energy.

Although the electric and magnetic realms may be inextricably linked, if one treats them as being separate then the electrical inductor can be taken to arise from a capacitor in the magnetic realm coupled by an antireciprocal transducer (gyrator) to the electric realm. A common inductor comprises a wire coil wound around a core with high magnetic permeability. Letting  $F_1$  be electric potential (J/C),  $F_2$  be magnetomotive force (MMF, measured in J/Wb),  $J_1$  be charge flow (C/s),  $J_2$  magnetic flow (rate of reorientation of magnetic dipoles, measured in Wb/s), and invoking Faraday's law for  $z_{12}$  and Ampere's law for  $z_{21}$ , one obtains the following two-port model for an ideal wire coil:  $z_{11} = 0$ ,  $z_{12} = -N$ ,  $z_{21} = N$ ,  $z_{22} = 0$ . The core serves as a magnetic capacitor, accumulating alignment (measured as Wb) of its (fixed number of) magnetic dipoles, leading to increase of potential energy (and MMF). The value of the magnetic capacitance ( $C_m$ , in Wb per unit MMF) is the

reciprocal of the magnetic reluctance. Thus a capacitor and a gyrator provide emulation of inertial impedance ( $i\omega N^2 C_m$ ) and momentum ( $N^2 C_m J_1$ ) in the electric realm. For physical realms in which inertia is negligible or non-existent (e.g., chemical, thermal, diffusional), which includes most of the physical realms associated with cellular biophysics, the ability to emulate inertia and kinetic energy would open the door to a range of dynamic behavior (e.g., resonance) not available with linear, passive systems employing potential energy alone — just as the inductor did for electrical circuit designers (see Table 1, Guillemin (1957)). The range of dynamic behavior of linear systems without inertia also can be extended by inclusion of active elements. This may be the basis, for example, of electrical resonances (believed by some to be involved in tuning) in various sensory cells (Crawford and Fettiplace, 1981; Zakon, 1986). On the other hand, the possibility of reciprocal transduction between mechanical structures outside the cell (e.g., via motile cilia, see Weiss, 1982) and the cell's electric realm opens the door to the possibility of translation of mechanical inertia to electrical inductance and incorporation of that inductance into an electric resonance.

A reciprocal or antireciprocal transducer operates equally well in both directions, passing free energy from the realm connected to port 1 to the realm connected to port 2 and vice versa. Typically, with an active transducer, the flow or potential at one port controls a flow of energy (from an independent source) at the other port. Such a transducer is expected to be neither reciprocal nor antireciprocal and therefore not to operate equally well in both directions (in fact it often does not operate at all in the reverse direction). Gated ion channels are biological examples of active, non-reciprocal transducers. Such devices evidently are involved, for example, in the cellular electrical resonances mentioned in the previous paragraph (Hudspeth and Lewis, 1988).

#### 14. Linear transformers and simple machines

When one is designing systems involving transducers, a consideration that often arises, especially with actuators, is how to maximize the power

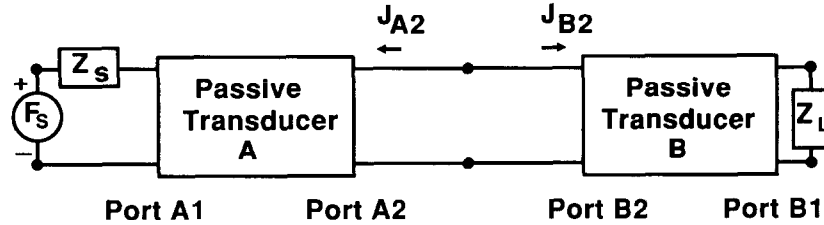


Fig. 4. A circuit representation of a transformer (rigidly-coupled, back-to-back passive transducers) connecting an independent potential source  $F_S$  (with its intrinsic impedance,  $Z_S$ ) to a load (with its intrinsic impedance,  $Z_L$ ). The rigid back-to-back coupling is represented by the constraint,  $J_{A2} = -J_{B2}$ , imposed by the circuit graph.

transferred through the device. This is accomplished by impedance matching, which in turn often is accomplished through use of another kind of device, often called a transformer. Transformers too can be modeled as two-port elements, but with both ports connected to the same physical realm. In many cases, transformers can be synthesized from two passive transducers connected back-to-back, tightly coupled in the intervening realm, a situation that can be modeled easily with two two-port elements connected in cascade (Fig. 4). For the ideal transducers described by Eqs. 21 and 22 the constitutive relationships for this cascade, when it is reduced to a single, equivalent two-port element, are represented by the following  $h$  parameters:

$$\begin{aligned} h_{11} &= 0 & h_{12} &= \frac{\lambda_{r1}}{\lambda_{r2}} & h_{21} &= 0 & h_{22} &= \frac{r_{r1}}{r_{r2}} \\ h_{21} &= -\frac{\lambda_{r1}}{\lambda_{r2}} & h_{22} &= 0 & h_{21} &= -\frac{r_{r1}}{r_{r2}} & h_{22} &= 0 \end{aligned} \quad (23)$$

In rigid-body mechanical realms, transformers of this type often fall into the class of devices known as simple machines (e.g., hydraulic press or jack, block and tackle, lever). For piston, pulley and semilever, the parameter  $\lambda$  (or its reciprocal, depending on which realm is depicted at port 1) is area, radius, and distance from end to fulcrum, respectively; and the ratio  $\lambda_1/\lambda_2$  in a simple machine constructed as a cascaded pair of such devices is the mechanical advantage. More generally, it can be labelled the transformer ratio. Eq. 15 can be used to obtain the impedance transformation through the cascaded pair:

$$Z_{dp} = \frac{\lambda_1^2}{\lambda_2^2} Z_L \quad (24)$$

The hydraulic jack or press is synthesized with two pistons rigidly coupled in the hydraulic realm — leading to a transformer in the translational mechanical realm. Two pistons rigidly couple in the translational mechanical realm, on the other hand, produce a transformer in the hydraulic realm. The middle ears of some lower vertebrates possess such devices, evidently transforming the (hydraulic/rigid-body mechanical) impedance of the inner ear to match the acoustic impedance of air (see Fig. 5). In the middle ears of mammals, a chain of semilevers (the ossicular chain) intervenes between the two pistons (the tympanum and the stapedial footplate). Given the large repertoire of passive transducers that are available (only a few of which have been mentioned in this paper), it is interesting to imagine other sorts of transformers that one might synthesize (e.g., an electrical transformer from back-to-back thermopiles).

### 15. Epilogue

I hope that this brief visit has convinced the reader that circuit theory provides a potentially useful framework in which to generalize and manipulate some of the elementary principles of classical physics, and that it will entice those not already familiar with the analytical and synthetic tools of circuit theory to read further on the subject.

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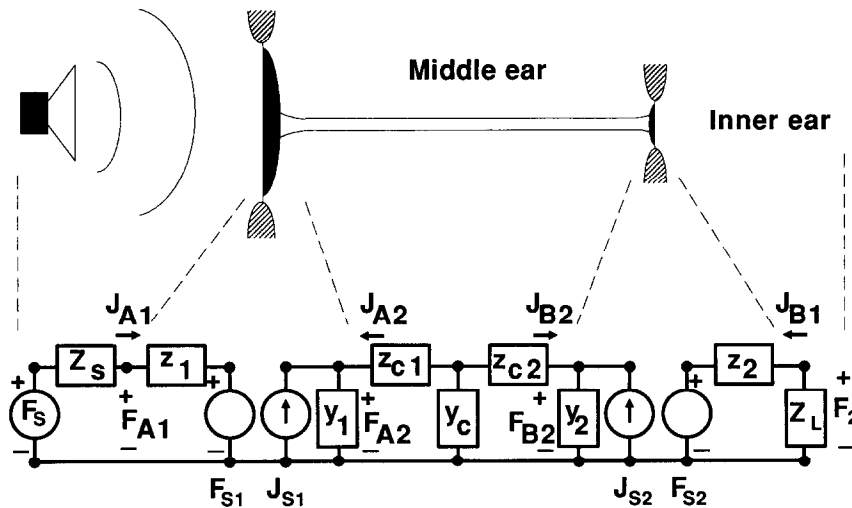


Fig. 5. A more realistic circuit model of a transformer. The transformer is represented by two versions of the lower model in Fig. 2, connected back to back but through an intervening structure (represented by the impedances  $z_{c1}$  and  $z_{c2}$  and the admittance  $y_c$ ) that is not perfectly rigid. The constitutive relationships for the dependent sources are  $F_{s1} = \lambda_1 F_{A2}$ ,  $J_{s1} = \lambda_1 J_{A1}$ ,  $F_{s2} = \lambda_2 F_{B2}$ , and  $J_{s2} = \lambda_2 J_{B1}$ . If this circuit represented the middle ear of a frog (comprising two pistons connected by a nearly-rigid rod), for example, then impedance  $Z_s$  could represent the acoustic impedance of the air,  $z_1$  could represent the combined elastic, inertial and resistive impedances of the external (left-hand) piston (the tympanum) when it is allowed to move freely, admittance  $y_1$  the compressibility of that piston when it is held rigidly in place, admittance  $y_c$  the compliance of the rod connecting the two pistons, impedances  $z_{c1}$  and  $z_{c2}$  the inertial impedance of that rod, admittance  $y_2$  the compressibility of the internal piston (at the oval window of the inner ear) when it is held rigidly in place, impedance  $z_2$  the combined elastic, inertial and resistive impedances of that piston when it is allowed to move freely (unimpeded by the rod or the inner ear), and impedance  $Z_L$  the driving-point impedance of the inner ear as seen from the oval window. In an ideal transformer,  $z_1$ ,  $z_2$ ,  $y_1$ ,  $y_2$ ,  $y_c$ ,  $z_{c1}$  and  $z_{c2}$  will be negligibly small. For consistency in the model, however, the two dependent flow sources should be shunted by a finite admittance, a finite impedance should be connected in series with the independent potential source  $F_s$  and the dependent potential source  $F_{s1}$ , and dependent source  $F_{s2}$  should have finite impedance connected across it. As  $z_1$ ,  $z_2$ ,  $y_1$ ,  $y_2$ ,  $y_c$ ,  $z_{c1}$  and  $z_{c2}$  become negligible, the driving-point impedance at port 1 ( $F_{A1}/J_{A1}$ ) will approach  $(\lambda_1/\lambda_2)^2 Z_L$ . The acoustic energy flow into the middle ear will be maximum when that driving-point impedance equals the complex conjugate of  $Z_s$ .

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## References

- Atkins, G.L., 1969, Multicompartmental Models for Biological Systems (Methuen & Co., London).
- Chua, L.O., Desoer, C.A. and Kuh, E.S., 1987, Linear and Nonlinear Circuits (McGraw-Hill, New York).
- Crawford, A.C. and Fettiplace, R., 1981, An electrical tuning mechanism in turtle cochlear hair cells. *J. Physiol. (Lond.)* 364, 359–379.
- Daniels, F. and Alberty, R.A., 1955, Physical Chemistry (Wiley, New York).
- Desoer, C.A. and Kuh, E.S., 1969, Basic Circuit Theory (McGraw-Hill, New York).
- Fox, R.W. and McDonald, A.T., 1978, Introduction to Fluid Mechanics (Wiley, New York).
- Gardner, M.F., and Barnes, J.L., 1942, Transients in Linear Systems (Wiley, New York).
- Guillemin, E.A., 1957, Synthesis of Passive Network (Wiley, New York).
- Hudspeth, A.J., and Lewis, R.S., 1988, A model for electrical resonance and frequency tuning in saccular hair cells of the bullfrog, *Rana catesbeiana*. *J. Physiol. (Lond.)* 400, 275–297.
- Karnop, D.C. and Rosenberg, R.C., 1975, System Dynamics: A Unified Approach (Wiley, New York).
- Kittel, C., 1958, Elements of Statistical Physics (Wiley, New York).
- Linville, J.G., and Gibbons, J.F., 1961, Transistors and Active Circuits (McGraw-Hill, New York).
- Mason, S.J., 1956, Feedback theory — further properties of signal flow graphs. *Proc. IEEE* 44, 920–926.



- Merhaut, J., 1981, *Theory of Electroacoustics* (McGraw-Hill, New York).
- Onsager, L., 1931a, Reciprocal relations in irreversible processes. I. *Phys. Rev.* 37, 405–426.
- Onsager, L., 1931b, Reciprocal relations in irreversible processes. II. *Phys. Rev.* 38, 2265–2279.
- Oster, G.F., Perelson, A.S. and Katchalsky, A., 1973, Network thermodynamics: dynamic modelling of biophysical systems. *Q. Rev. Biophys.* 6, 1–134.
- Quarles, T., 1989, *SPICE3 Version 3C1 User's Guide* (University of California — Electronics Research Laboratory, Berkeley).
- Thoma, J.U., 1990, *Simulation by Bondgraphs* (Springer-Verlag, Berlin).
- Weiss, T.F., 1982, Bidirectional transduction in vertebrate hair cells: a mechanism for coupling mechanical and electrical processes. *Hearing Res.* 7, 353–360.
- Yourgrau, W., van der Merwe A. and Raw, G., 1982, *Treatise on Irreversible and Statistical Thermophysics* (Dover Publications, New York).
- Zakon, H.H., 1986, The electroreceptive periphery, in: *Electroreception*, T.H. Bullock and W. Heiligenberg (eds.) (Wiley, New York) pp. 103–156.