A Bond Graph Model of Outer Hair Cell Active Force Generation

C. Wangcharoenrung* and R.G. Longoria†
The University of Texas at Austin
Austin, TX 78712

Keywords: Hair Cells, Electromotility, Electrophysiology

Abstract

A bond graph model is used to study the outer hair cell, a hair cell of type II, and its active force generating mechanism. The outer hair cell is considered one of the most important parts of the vertebrate sensory transduction mechanism. For example, in the mammalian hearing system, the outer hair cell provides an active force believed to be responsible for the sharp tuning characteristics of the cochlea. Many studies have been conducted to understand the behavior of the outer hair cell, and electric circuit analogs have been proposed to model the dominant mechanisms. It is proposed and demonstrated here that a bond graph model can provide a systematic and unified representation of the interacting mechanical, electrical, and biochemical behavior in hair cells.

In this paper, a model of a hair cell is formulated and expressed in bond graph form. This representation is used to arrive at simulations of hair cell performance that can be compared with observed behavior and results from experiments drawn from the literature. These comparisons are used to help verify the model and to adjust physical parameters. We have found that a simple two-port piezoelectric model of the membrane can provide reasonable results, but only if we specify unrealistic parameter values. This study suggests that extensions to this model are required, and these are briefly reviewed in this paper. This evolving hair cell model will be used to study the unique capabilities observed in this sensory transduction mechanism, which might serve as a model for new engineered sensing devices.

1 Introduction

Hair cells (see Figure 1) are an extremely sensitive mechano-electroreceptor type of cell found mostly in vertebrate acousticolateral system. They are grouped in specialized sensory regions such as in the organ of corti (the organ of hearing), the crista ampullaris of the semicircular canals (the vestibular apparatus), and many others [1]. These organs play a critical role in diverse natural sensory functions such as sensing body motor activity and body coordination, sensing gravity, and detecting pressure fluctuations in the air. Although these organs have different and specific functions, they have a similar structure and are believed to be evolved from a common "original" organ. The reliance of these sensory organs on the basic hair cell has inspired many physiological studies. The study described in this article is similarly inspired, and seeks to integrate existing knowledge using a bond graph model basis. By building a structured model in this way, it is anticipated that insight can be gained into how the basic hair cell achieves its most useful transduction functions, as well as how these functions depend on the hair cell constituent components.

There are two kinds of hair cells. The inner hair cell (IHC) or cell of type I, and the outer hair cell (OHC) or cell of type II. Inner and outer hair cells take their name from their position at the inner and outermost part, respectively, on the basilar membrane of the organ of corti in human cochlea. Generally, the two have a similar structure, although they perform a different function in sensory transduction.

As shown in Figure 1, the outer hair cell is a cylindrical shaped cell that has a group of cilia (or hairs), made from actin filament, protruding from the apical end. These cilia are arranged regularly, often in a hexagonal (diamond) pattern. In human cochlea, the outer hair cell structure is fixed only at its basal part with Deiter’s cell. However, the apical part of the cell is sealed by a membrane called the reticular lamina. The primary sensing function of the hair cell is to convert the motion (rotation) of the hair bundle into electrical potential or impulses transmittable by the nervous system. Deflection of a hair bundle toward the kinocilium will result in depolarization, which increases the nerve's firing rate, while deflection away from the kinocilium results in hyperpolarization, which decreases the firing rate of nerve.

Of particular interest in this study is the "electromotility" of the outer hair cell, which characterizes its ability to elongate or contract longitudinally in response to changes in transmembrane potential (depolarization and hyperpolarization).
This mechanism is believed to be a basis for active force generation and allows outer hair cells to modulate the bundle deflection (thus providing a sort of self-modulation). This active force generation in the outer hair cells of cochlea has been considered to be the key underlying factor responsible for the sharp tuning mechanism in the mammalian cochlea. For this reason, electromotility has received considerable attention in the field of otolaryngology. A number of current research studies are underway in this field to determine the origin of the sensory mechanism. This includes formulation of a suitable mathematical model, such as the work by Mountain and Hubbard [11], who have studied the hair cell mechanism using a piezoelectric material model, or Spector, et al [14], who take a more phenomenological approach based on an elasto-electric model.

The system behavior depends on coupled microscale processes, and is generally difficult to extract due to the need to bring together disparate information available from various studies the literature. Hair cell behavior is not yet completely understood. Any modeling effort must rely on partial information, especially if quantitative model studies (i.e., simulations) are to be conducted. A dynamic simulation model of active force generation would provide insight into the basic mechanisms at work in this sensory system, and possibly lead to an understanding for how such behavior can be achieved using other (synthetic) types of electromechanical transduction. This paper describes the formulation and interconnection of sub-models used to describe the overall hair cell behavior. The ability of the final model to represent observed hair cell behavior is evaluated using simulation test cases. Several methods for modeling electromotility using theory of piezoelectricity are presented, compared, and discussed to find a simple and suitable approach for modeling membrane transduction behavior.

1.1 Mechanical Vibration of Outer Hair Cell

A model of the mechanical characteristics of the outer hair cell will capture the longitudinal vibration, and a basic form can be visualized as in Figure 2. In order to simplify this model, the following assumptions are made: 1) all cilia move together as one bundle, 2) the cilia bundle rotate at the base which has rotational stiffness and some damping, 3) the cilia bundle has negligible mass compared to the cell body, 4) the hair cell's body can be lumped as a single point mass, and 5) the hair cell's plasma membrane has an axial stiffness (that also depends on transmembrane potential).

![Figure 2: Diagram showing a hair cell as a mechanical vibration system. Symbols included are: l, length of hair bundle, m, effective mass of cell body, k_\theta, rotational stiffness of cilia, k_c, linear stiffness of cell body and membrane, b_\theta, rotational damping ratio of cilia bundle, and b_c, linear damping ratio of plasma membrane.](image)

Based on the model in Figure 2, a bond graph can be drawn as shown in Figure 3. The forced motion of the hair cell bundle is modeled here using a simple linkage, represented by a simple modulated transformer with modulus, m = l \cdot \sin(\theta).

Parameters for this mechanical system model, such as membrane stiffness, can be obtained from theory and experiments as described in the literature (e.g., Iwasa [9]). However, several parameters, such as the effective mass and damping values cannot be found and must be estimated using the model.

1.2 Ionic Gating Mechanism

Hair cells rely primarily on an ionic gradient in the surrounding fluid in order to create an action potential. The apical
part of the cell is bathed in endolymph, a lymph fluid rich in potassium ion (K⁺), and the body of the cell is bathed in perilymph, another fluid rich in calcium ion (Ca²⁺). The reticular lamina is a membrane that separates these two fluids. From a modeling perspective, it is possible to represent this gating mechanism as a dissipative switching mechanism modeled using resistive elements.

When the stereocilia deflect (i.e., in activation direction), whether by direct forcing of fluid or indirectly by basilar membrane motion, the tip links between cilia stretch to open the potassium channel at the apical end of the cell. This opening allows potassium ions (K⁺) to flow from the high concentration of endolymph into the cell. This increase in potassium ions inside the cell is responsible for increasing the cell’s transmembrane potential, which depolarizes the cell resulting in an increase in the afferent nerve firing rate. The higher potential of the cell also results in activation of voltage-activated calcium ions (Ca²⁺) channel, allowing calcium ions to flow inside the cell. Hair cells then use calcium ions as a medium to open the calcium-activated potassium channel that opens to perilymph allowing deposited potassium ion to flow out. As soon as the loss of potassium ions flowing through calcium gates exceed the inward flow of potassium though the mechanical gates, the hair cell starts to repolarize. This decreases the calcium flow through the voltage gate, decreasing the nerve firing rate. Excess calcium ions are then pumped out by specific calcium ion ATPase-pump, allowing the cell to completely repolarize and reset to its new position, until the mechanically-activated gate kicks in to start another cycle of transduction. The mechanism can be visualized as shown in Figure 4.

Figure 3: Bond graph model of hair cell mechanical vibration.

Figure 4: Diagram showing ion channels of the hair cell. 1) Top channel is mechanical (deflection) activated potassium ions channel, 2) Top right channel is potential activated calcium channel, 3) Bottom right channel is calcium activated potassium channel, and 4) Left channel is specific calcium ion pump. From Hudspeth [6].

Now, a function representing the gating mechanism has to be made, and an analogy to common fluid valves is helpful. Each ionic channel can be modeled using simple modulated resistors. First, for the apical channel, the angle of deflection of the cilia bundle is related to how much the ionic channel at the apical part opens to allow an inflow of potassium ions. It is assumed that there is one channel in each cilia, and that a channel is either fully open or fully closed. The more a hair bundles deflects toward the kinocilium activation direction, the more chance that each channel will open, thus decreasing the total channel resistance.

A probabilistic approach (similar to Hodgkin and Huxley [7]) will be used to describe the gating mechanism. To illustrate, consider that \( x \) is a measure of open channels, and that its probability density function, \( f(x) \), takes a Gaussian form,

\[
f(x) = \frac{1}{\sigma \sqrt{2\pi}} \exp \left( -\frac{(x-\mu)^2}{2\sigma^2} \right),
\]

where \( \sigma \) is the standard deviation, and \( \mu \) is the mean. Assume that \( x \) (which gauges the probability of open channels) is linearly related to angle of deflection, \( \theta \). Then the probability is used to scale the ratio of channel conductance to the maximum channel conductance, \( g/g_{\text{max}} \), so that,

\[
g = g_{\text{max}} \left[ \frac{1}{2} + \frac{1}{2} \operatorname{erf} \left( \frac{a\theta + b - \mu}{\sqrt{2}\sigma} \right) \right].
\]

In this relation, \( a \) and \( b \) are constants that can be related to this model by experiment (e.g., see van Emst et al. [15]). The estimated channel conductance function is plotted in Figure 5.

For the basal ionic channel, we must estimate how much the channel opens when a given amount of potassium ions are stored in the cell body. There are two main factors that drive ion flow between intracellular fluid and extracellular fluid.
A balance between drive forces described by Fick's law for concentration and a field law (of ionic mobility) for potential gives rise to the Nernst equation. This widely used relation estimates the resting transmembrane potential of a cell,

$$E_m = \frac{RT}{Z_p} \ln \left( \frac{[C_e]}{[C_i]} \right),$$

where $E_m$ is the equilibrium transmembrane potential, $[C_e]$ is the extracellular fluid concentration of ions, $[C_i]$ is intracellular fluid concentration of ions, $R$ is the universal gas constant (8.314 Jules/K ), $T$ is absolute temperature in Kelvin, and $F$ is Faraday's constant of 96487 abs coulomb/gram eq, and $Z_p$ is valence of ion.

In the case of hair cells, the dominant ion responsible for transmembrane potential is potassium, because it has a higher channel permeability than any other ion species. Other species can then be ignored to arrive at an acceptable estimate of transmembrane potential. Following Weiss and Leong [16], a linear relation is assumed to exist between concentration from Nernst equation and probability that ions are stored inside and outside of the cell body. Hence, a probability equation of the form,

$$\frac{P_i}{P_o} = \exp \left( -\frac{E_m F Z_p}{RT} \right),$$

relates $P_i$ and $P_o$, which are probabilities that ions are inside and outside, respectively. If a linear relation is assumed to exist between the probability and channel conductance, then,

$$\frac{g}{g_{max}} = \left[ 1 + \exp \left( -\frac{E_m F Z_p}{RT} \right) \right],$$

where $g$ and $g_{max}$ are the basal ionic channel conductance and maximum basal ionic channel conductance, respectively. We simplify the equation to,

$$R(E_m) = \frac{\gamma}{g_{max}} (1 + e^{-\beta E_m}),$$

where $R$ is the channel resistance, $\gamma$, and $\beta$ are constants that can be arrived at from experimental data for a specific kind of cell. Hodgkin and Huxley [7] provide some discussion about these constants.

### 1.3 Hair Cell Simple Circuit Model

A circuit model first developed by Hodgkin and Huxley in 1952 [7] for cardiac muscle has been used as a guide for building a circuit model for the hair cell. A critical assumption is that the concentration difference forces the plasma membrane, which is a dielectric lipid bilayer, to behave as a capacitor that separates electrical charge. Ion channels that are embedded inside the membrane, as discussed above, can be considered as a resistive element in series with a bias voltage source. The voltage source is modeled to have a voltage equal to the resting Nernst potential, with a polarity that opposes the ion flow due to concentration. In this way, a simple circuit model for the electrical characteristics of the hair cell, considering only potassium, can be formulated as shown in Figure 6.

![Figure 6: Equivalent circuit diagram of hair cell ion flow, considering only potassium. The model uses perilymph potential as a reference.](image)

### 1.4 Plasma Membrane Electromotility

Electromotility in the outer hair cell, as described earlier, has been under extensive study for many years. However, until recently there has been no definite agreement as to how the process actually occurs. For example, one recent theory proposes that the plasma membrane of the hair cell is composed
of a special motor protein called "prestin" [17]. Another theory suggests that the membrane is folded in a similar fashion to the folding mechanism of red blood cells [12].

The method first considered here, because of the relative convenience of integration into a bond graph model, is a two-port, one-dimensional capacitive element (e.g., see Busch-Vishniac and Paynter [3]). In this model,

\[ V = \frac{q(d_0 + x)}{\varepsilon A}, \]

where \( \varepsilon \) is the relative dielectric constant of the membrane, \( A \) is the membrane area, \( d_0 \) is the initial membrane thickness, \( x \) is the dynamic change in thickness, and \( V \) is potential difference. Since,

\[ \frac{dE}{dq} = V = \frac{q(d_0 + x)}{\varepsilon A}, \]

then,

\[ E = \int \frac{q(d_0 + x)}{\varepsilon A} dq = \frac{q^2}{2\varepsilon A} + \phi(x). \]

Assume in this case that \( \phi(x) \) is the normal electric strain energy, which is \( \phi(x) = x^2/2C_E \). Then, an equation for energy stored in the plasma membrane, in the case where polarization energy is ignored, is given by,

\[ E = \frac{q^2}{2\varepsilon A} + \frac{x^2}{2C_E}, \]

which makes,

\[ F = \frac{\partial E}{\partial x} = \frac{q^2}{2\varepsilon A} + \frac{x}{C_E}, \]

and,

\[ V = \frac{\partial E}{\partial q} = \frac{q(d_0 + x)}{\varepsilon A}. \]

These constitutive relations couple the mechanical and electrical domains in the hair cell.

In reality, the electromotility effect has been found to exhibit piezoelectric material behavior. Indeed, methods for modeling this piezoelectricity have been considered to quantify the electromotility effect of the hair cell's plasma membrane, such as the electromotility model of Mountain and Hubbard [11]). This type of model is discussed in a subsequent section.

1.5 Interconnecting the Model Elements

A 'baseline' model is formed by connecting all the sub-models discussed up to this point. A complete bond graph model of the outer hair cell is shown in Figure 7. The left side of the two-port capacitive (C) element represents the mechanical characteristics of the hair cell, and the right side represents the ion flow model. There is a signal bond connecting the two energy domains, representing how the angle of the hair bundle deflection affects how much the potassium channel at the apical part opens. The additional resistive element, \( R_{\text{nubber}} \), included in this model represents damping in the fluid structure of the cell. It also helps ensure integral causality on the storage elements, facilitating the equation derivation.

2 Simulations and Discussions

The bond graph model was used to formulate a Simulink\textsuperscript{®} model for simulation in Matlab\textsuperscript{®}. These simulation results used the baseline two-port one-dimensional capacitive model for the hair cell plasma membrane.

Firstly, the model was tested for an ability to simulate hair cell action potential. Results from testing the electrical sub-model of Figure 6 are shown in Figure 8. The model predicts a resting potential of about \(-35 \text{ mV}\) which is realistic. After 35 milli sec, the hair bundle has been deflected to about 0.8 radian (45 degree), and this initiates a change in resting potential in a pulse form very similar to action potential trends reported in the literature. Note that a transport delay has been added to the basal ion channel to simulate an effect observed in a basal ion channel that senses calcium as a second messenger.

![Figure 8: Simulation of receptor potential response to impulse deflection in bundle angle](image_url)

Figure 8: Simulation of receptor potential response to impulse deflection in bundle angle

Next, the whole system is simulated to determine the ac-
tive force generation by the plasma membrane. A sinusoidal force with amplitude 1 milli-Newton and a frequency of 70 Hz pushes positive downward as an input, after a 40 millisecond resting period. The simulation result is summarized in Figure 9 below.

From these simulation results, it is seen that the model predicts the effect of electromotility in a fashion similar to that observed in vivo [5]. When the membrane is depolarized (has a positive potential), the membrane Coulombic force is generated in a direction that contracts the membrane. However, the model incorrectly predicts even more contraction in the hyperpolarization region.

These preliminary results found using the two-port one-dimensional C element allow basic trends to be derived rather easily. However, the use of this model form results in a quantitatively unrealistic prediction for the active force generation. Specifically, equations (11) and (12) have been used in this initial simulation model. These equations are not really suitable in this situation due to three factors. First, the transmembrane potential is in a transverse direction and the hair cell contracts and expands in a longitudinal direction, so clearly the one-dimensional model is not appropriate. Second, the polarization energy that has been ignored appears to play a significant role in active force generation in the hair cell plasma membrane. Third, force generation due to Coulombic forces is always in the same direction, regardless of the direction of current flow across membrane. Equation (11) predicts dynamic effects mainly due to interaction between Coulombic and strain energy forces.

In real hair cells, active force generation, according to theory and experiment such as that of Iwasa [9], will be in the region of 0.1 nano-Newton with deflections of 1.25-1.56 nanometer per millivolt. These relative magnitudes can be achieved using the 1-D capacitive model by 'tuning' the parameters. In the simulation results shown, for example, the stiffness of the piezoelectric membrane has been increased to prevent it from excessively compressing due to the input forcing. This occurs because the membrane is very thin. By making this unrealistic parameter adjustment, the mechanical structural effects are too stiff and it is found that the reaction forces generated by membrane stiffness are over predicted.

3 Extended Model for Plasma Membrane Electromotility

The unrealistic results found using the one-dimensional two-port capacitive model of the plasma membrane prompts consideration of a two-dimensional model three-port C-element. Two approaches can be considered for this application: an impedance matrix formulation and a strain energy approach.

The impedance matrix has been commonly used to model general (inorganic and organic) piezoelectric materials. This approach describes material piezoelectric characteristics using an impedance matrix (e.g., Davi [4]) and takes the form,

\[
\begin{bmatrix}
T \\
d
\end{bmatrix} = \begin{bmatrix}
C(e) & -H \\
H^T & K(e)
\end{bmatrix} \cdot \begin{bmatrix}
e \\
e^T
\end{bmatrix}.
\] (13)
where $E$ in this case is the modulus of elasticity of the material, $h$ is the effective thickness of the shell or plasma membrane thickness, $v$ is the Poisson ratio, $l_0$ is initial length of the hair cell, and $r_0$ is the initial radius of the hair cell. The force is defined downward positive in the $x$ direction and inward positive in the $r$ direction.

The piezoelectric tensor field $g$ is usually determined by empirical study of a specific material (e.g., Ikeda [8]). Initial study has shown that it might be possible to use organic polymer characteristics to approximate the membrane piezoelectric properties, due to structural similarity. However, a simple exponential function can also be used to approximate the tensor $g$ as seen in Spector et al [14],

\[
\begin{align*}
T(x, t) &= \begin{cases} 
\frac{a}{1-\exp(-b AV)}, & \text{when } AV > 0 \\
\frac{a}{1-\exp(-b AV)}, & \text{when } AV < 0 
\end{cases} 
\end{align*}
\]

and,

\[
\begin{align*}
R(x, t) &= \begin{cases} 
\frac{a}{1-\exp(-b AV)}, & \text{when } AV > 0 \\
\frac{a}{1-\exp(-b AV)}, & \text{when } AV < 0 
\end{cases} 
\end{align*}
\]

Note that this equation must be modified to fit a capacitive constitutive relation between voltage and charge. Also, only the potential gradient in the radial ($e_r$) direction is considered. The constants, $a, a, b, b, a, b, b, b$ have a requirement for smoothness as [14],

\begin{align*}
b &= \frac{a b}{a_r}, \\
b &= \frac{a b}{a_r}. 
\end{align*}

Finally, $\beta^{(e)}$ can be considered for this application in only one (radial) dimension to be a simple constitutive relation for a concentric cylinder that has a capacitance given by,

\[
C = \frac{2\pi\varepsilon_0\varepsilon_r}{\ln(b/a)} L.
\]

where $\varepsilon_0$ and $\varepsilon_r$ are the dielectric constants for free space and relative dielectric constant of plasma membrane, respectively. The constant, $b$, is the outer radius, $a$ is the inner radius ($b - a$ is membrane thickness), and $L$ is the effective length of the outer hair cell.

Another three-port two dimensional model that can be considered for this application is based on expansion of the one-dimensional model to two dimensions that includes the polarization energy. If equation (8) is modified for a concentric cylinder,

\[
\frac{\partial E}{\partial y} = V = \frac{q}{2\pi\varepsilon_0\varepsilon_r(l_0 - x)} \cdot \ln \left[ \frac{r_0 + h + r}{r_0} \right].
\]

The method applied in the first approach is now considered with strain energy in two dimensions. The Petrov theory
of flexoelectricity for active transport, which assumes a linear relationship between membrane polarization enthalpy and membrane deformation (as presented in Raphael et al. [12]) leads to,

\[ Ph = f \cdot c \cdot e, \]  

where, \( f \) is flexoelectric coefficient, and \( c \) is membrane curvature. If a linear relation is assumed between membrane curvature and total deflection, as well as between field and transmembrane voltage, the total polarization energy can be expressed as,

\[ E_p = \frac{\alpha x}{2 \pi \epsilon_0 \epsilon_r (l_0 - x)} \ln \left[ \frac{r_0 + h + r}{r_0} \right] q, \]  

where \( \alpha \) is a constant related to flexoelectric coefficient. In this way, an equation for total energy stored in plasma membrane is found to be,

\[ E_{\text{mem}} = \frac{\ln \left[ \frac{2 \pi k_{mn}}{2 \pi \epsilon_0 \epsilon_r (l_0 - x)} \right]}{2} \left( \alpha x + \frac{q}{2} \right) + \frac{1}{2} k_1 x^2 + \frac{1}{2} k_2 x^2 + k_2 x r, \]  

where \( k_{\text{mn}} \) is the stiffness of the material that can be inferred from Equation (15), yielding a final set of constitutive relations,

\[ F_r = \frac{\partial E}{\partial r} = \frac{q \cdot (\alpha x + \frac{q}{2})}{2} (r_0 + h + r) \epsilon_0 \epsilon_r (l_0 - x) + k_1 x + k_2 r, \]  

and,

\[ V = \frac{\partial E}{\partial h} = \frac{\ln \left[ \frac{2 \pi k_{mn}}{2 \pi \epsilon_0 \epsilon_r (l_0 - x)} \right]}{2} \left( \alpha x + \frac{q}{2} \right) + \frac{1}{2} \frac{\ln \left[ \frac{2 \pi k_{mn}}{2 \pi \epsilon_0 \epsilon_r (l_0 - x)} \right]}{4 \pi \epsilon_0 \epsilon_r (l_0 - x)} \cdot q. \]  

These formulations are currently under study as extended constitutive relations for a three-port capacitive bond graph element model for plasma membrane that considers polarization energy. More work is required to determine whether these models may provide the improvement sought over the original one-dimensional two-port representation. The constitutive relations as presented here show that these extended models are consistent with a bond graph formulation, and can be integrated into the existing hair cell model. This is the topic of ongoing work, which will also require careful parameterization of these model relations by studying results from ongoing empirical research in this field.

4 Conclusion

Hair cells are responsible for many important sensory functions in animals. Electromotility, the ability of outer hair cells to actively generate force and to subsequently modify its own vibration response, is a mechanism that sets it apart from normal passive sensory systems. Understanding the underlying mechanisms that govern the inherent dynamics may improve understanding of how this mechanism is controlled locally and remotely, and this paper shows how a bond graph model provides a unified representation for the hair cell model.

A key issue is demonstrated through application of a basic two-port one-dimensional capacitive model in the overall hair cell model. While it is found that this allows the model to satisfactorily predict expected trends in electromotility, the quantitative results are not accurate. Extended models may be required, and these have been presented to show that a two-dimensional model, also consistent with the bond graph formulation, can be effectively integrated.

The 'engineering' motivation for this study is to use the knowledge gained by a model of hair cell sensory transduction and related control mechanisms to provide insight into active sensor designs. By modeling the outer hair cell using common engineered sensor elements, such as piezoelectric materials, a guide for engineered sensor systems with the type of favorable characteristics exhibited by hair cells may be formulated.

Figure 10: Table showing list of variables used for initial simulation. Note that the value of mechanical compliance of plasma membrane is unrealistically adjusted as discussed in the results.

References


THE PROCEEDINGS OF THE

2003 International Conference on Bond Graph Modeling and Simulation (ICBGM 2003)

Edited by
Jose J. Granda
Francois Cellier

Simulation Series

Volume 35
Number 2

Orlando, Florida • Marriott Orlando Airport

January 19 - 23, 2003

SCS


Sponsored by the Society for Computer Simulation