Abstract—Whiskers are widely used by many animal species for navigation and texture discrimination. This paper describes Darwin IX, a mobile physical device equipped with artificial whiskers, the behavior of which is controlled by a neural simulation based on the rat somatosensory system. During its autonomous behavior, Darwin IX is able to discriminate among textures in its environment and learns to avoid textures that are paired with aversive events.

I. INTRODUCTION

Haptic sensory information provided by mystacial vibrissae (whiskers) allows the rat to discriminate among different textures in its environment [8], [13]. Although whisker-based perception lacks the fine resolution and long range of vision, whiskers have the advantage of allowing navigation and discrimination in the dark. Previously, studies have focused on texture discrimination or contact localization by fixed whiskers or whisker arrays [6], [10], [14], or obstacle avoidance by mobile robots equipped with whiskers [3], [9].

To explore how haptic data may be used to discriminate among textures during autonomous behavior, we constructed Darwin IX, a mobile physical device equipped with artificial whiskers and a simulated nervous system based on the neuroanatomy of the rat somatosensory system. We show that neuronal units with time-lagged response properties, together with the selective modulation of neural connections strengths, provide a plausible neural mechanism for the spatiotemporal transformations of sensory input needed for both texture discrimination and selective conditioning to textures.

Darwin IX is the latest in a series of ‘brain-based devices’ (BBDs) that have been constructed over the last 12 years [5], [1], [11]. All BBDs in the Darwin series have the following attributes: 1) An embodied morphology that allows for active exploration in a real-world environment, including sensors such as proximity sensors and artificial whiskers. 2) A neural simulation to control the BBD’s behavior, incorporating detailed neuroanatomy and neurophysiology based on vertebrate nervous systems. 3) A value system that signals the salience of environmental cues and that modulates plasticity in the nervous system resulting in modification of the device’s behavior. These features result in a system that adapts its behavior via conditioning to become increasingly successful in coping with the environment.

In our experiments with Darwin IX, the device autonomously explored a walled environment containing two distinct textures each consisting of patterns of pegs embedded in the walls. It became conditioned to avoid one of the textures by association of this texture with an innately aversive simulated ‘foot-shock’. Darwin IX demonstrated its conditioned behavior by freezing and then moving away from walls containing the texture corresponding to the aversive stimuli.

II. METHODS

Darwin IX consists of a mobile robotic base containing IR proximity sensors, custom-built whisker arrays, and a cluster of workstations that run the simulated nervous system and control the device’s behavior (Fig. 1). The cluster consists of six 1.4 GHz Pentium IV workstations running Message Passing Interface (MPI) parallel software under the Linux operating system. One workstation receives whisker and IR input information, and transmits motor commands, via an RF modem. A microcontroller (PIC17C756A) onboard the base samples input and status from the sensors and controls RS-232 communication between the robotic base and the workstations, via a wireless modem.

During each simulation cycle of Darwin IX, sensory input is processed, the state of the neural simulation is updated, and motor output is generated. In our experiments, execution of each cycle requires approximately 100ms of real time.
Fig. 2. A. Detail of a whisker array: The top (T), middle (M), and bottom (B) whiskers in the column are labeled; these whiskers provide input to the neural simulation. B. Schematic of textures T1 and T2. Each texture consists of pegs embedded in a wall; pegs are aligned in rows corresponding to the whiskers in a column. Pegs in the top row deflect the top whisker (T), and similarly for pegs in the middle row (M) and the bottom row (B).

A. Artificial whisker design

Each whisker array consists of seven whiskers arranged in a column of three and a row of five (see Fig. 1 (inset) and Fig. 2). Whisker columns supply input to the simulated nervous system, while whiskers in the rows support innate avoidance and wall following behaviors (see section B. Innate behavior). Each whisker consists of two 4cm by 0.63cm polyamide strips, adhered back-to-back, that are responsive to bend (Jameco, CA). These strips are typically used as strain sensors in devices such as virtual reality gloves. Each strip has 20 resistive areas embedded regularly along its length, providing a resistance of \( \sim 10\)KΩ when the strip is unbent and \( \sim 50\)KΩ when strip is maximally bent. Each strip detects bending in only one direction, hence the back-to-back arrangement. Voltage signals from each pair of strips (i.e., a whisker) are converted to a single signal ranging from 0V (maximum deflection in one direction) to 5V (maximum deflection in the opposite direction). These voltages are converted into digital signals, ranging from 0 to 256, by a 12-bit analog-to-digital converter at a sample rate of 40Hz. During each simulation cycle of Darwin IX a ‘packet’ of 4 signals for each whisker is received by the neural simulation. For whisker \( w_k \), at simulation cycle \( t \), the corresponding packet is \([w_{k1}(t), w_{k2}(t), w_{k3}(t), w_{k4}(t)]\), where \( w_{k4}(t) \) is the most recent. The first signal in each packet, \( w_{k1}(t) \), which we call the ‘current whisker value’, is used for guiding Darwin IX’s wall following behavior; all four signals provide input to the neural simulation (see section D. Whisker input and lag cells).

B. Innate behavior

Darwin IX is equipped with innate behavioral responses. The default behavior of Darwin IX is to move forward in a straight line at a speed of \( \sim 8 \)cm/sec. If Darwin IX approaches a wall head-on to within a distance of \( \sim 4 \)cm, an avoidance response is triggered; the device stops, backs up \( \sim 10 \)cm, and then turns \( \sim 30 \) degrees away from the wall before resuming default behavior. Avoidance responses are triggered by two IR sensors, one facing front-left, and the other facing front-right. Darwin IX has an innate freezing/escape response which is triggered by a simulated ‘foot-shock’, which is registered when a downward-facing IR sensor at the front of the device detects a reflective construction paper (‘foot-shock pads’) on the floor of the arena. This response consists of continued movement for 55 simulation cycles \((\sim 5.5s)\), freezing for 40 cycles \((\sim 4s)\) then a turn away from the wall by an angle randomly chosen from the interval \([\pi/4, 3\pi/4]\).

Darwin IX also has an innate wall following capability such that, on encountering a wall, the device moves parallel to the wall at a distance suitable for the detection of embedded textures. Wall following is based on signals from the backmost (BK), the ‘middle’ whisker, which is lowest of the vertical stack (MD), and the frontmost (FT) on each side (see Fig. 1, inset). For each of these whiskers, a running average of the current whisker value \( \overline{w} \) is maintained over 75 simulation cycles. This average is updated at every cycle except when the current whisker value differs by more than 10 from the corresponding average (signifying whisker deflection; recall that the range of the current whisker value is 0-255). For each whisker on each side, a ‘deflection’ value \( \Delta w \) is calculated as:

\[
\Delta w_{BK}(t) = |w_{BK1}(t) - \overline{w}_{BK}(t)|
\]

\[
\Delta w_{MD}(t) = |w_{MD1}(t) - \overline{w}_{MD}(t)|
\]

\[
\Delta w_{FT}(t) = |w_{FT1}(t) - \overline{w}_{FT}(t)|
\]

Wall following of a left(right) wall is triggered when any deflection value for the left(right) whiskers exceeds 15. During each cycle of wall following, adjustments are made to the speed of the wheel furthest from the wall (the contralateral wheel); the other (ipsilateral) wheel remains at the default speed of \( W_{def} = 35 \). Contralateral wheel speeds are set using:

\[
W_{speed} = W_{def} - \text{back} - \text{mid} - \text{front}
\]

where \( \text{front} = 0.25(\Delta w_{FT}) \), \( \text{mid} = g_w(\Delta w_{MD} - \varphi_w) \), and \( \text{back} = g_w(\Delta w_{BK} - \varphi_w) \), and where \( \text{mid} \) and \( \text{back} \) are bounded in the range \( \pm 5 \), and \( g_w \) (a scaling factor) and \( \varphi_w \) (a threshold) are chosen according to the physical response characteristics of the whiskers (see Table I). Additionally, \( g_w \) varies according to the sign of the corresponding \( \Delta w \) such that there is a bias in favor of turning towards a wall (see Table I, columns 4 and 5).

C. Neuroanatomy

Darwin IX’s simulated nervous system contains areas analogous to the somatosensory pathway in the rat brain, specifically the (ventromedial) nuclei of the thalamus, and primary and secondary somatosensory areas (in our model, \( Th \rightarrow S1 \rightarrow S2 \)). Areas \( S1 \) and \( Th \) are subdivided into left (L) and right (R) regions and further into ‘top’ (T), ‘middle’ (M) and ‘bottom’...
of ascending neuromodulatory systems in that it is triggered by salient events, influences large regions of the simulated nervous system (see section F. Synaptic plasticity), and persists for several cycles [16].

D. Whisker input and lag cells

Whisker input to the neural simulation is provided by transforming each whisker packet into a vector of ‘difference values’ according to:

\[ \text{diff}_k = [w_{k4}(t) - w_{k3}(t), w_{k3}(t) - w_{k2}(t), w_{k2}(t) - w_{k1}(t), w_{k1}(t) - w_{k4}(t-1)] \]  

(5)

for whisker \( w_k \) at simulation cycle \( t \). These values from the whisker in each column provide input to the corresponding subregions of area \( Th \).

Each subregion of area \( Th \) contains 20 ‘lag’ cells; neuronal units which respond to input with cell-specific time delays (cells with similar properties exist in the visual thalamus of the cat [15]). Each lag cell is characterized by an internal state \( s_i(t) \), an output \( \psi_i(t) \), and a cell-specific lag parameter set to be \( \psi_i = \frac{w_i}{T} \), \( i \in \{1, 2 \ldots 20\} \) for cell \( i \) in each subregion. When triggered by a whisker deflection, the internal state \( s_i(t) \) of cell \( i \) in the corresponding subregion increases at rate determined by the lag parameter \( \psi_i \). When this internal state reaches a threshold, the cell begins to emit an output signal and \( s_i(t) \) is reset to zero. Because of differences in \( \psi_i \) among lag cells, each whisker deflection evokes a wave of activity in the corresponding subregion, with some cells firing shortly after deflection and the remainder firing with gradually increasing delays (see Fig. 3, inset).

Specifically, \( s_i(t) \) in the subregion corresponding to whisker \( w_k \), is updated according to:

\[
s_i^{\text{in}}(t+1) = \begin{cases} 
0.2 & s_i^{\text{in}}(t) < 0.2, \text{diff}_k(t) > 3.0 \\
0 & s_i^{\text{in}}(t) \geq \sigma_i^{\text{fire}} \\
(1 + \psi_i)(s_i^{\text{in}}(t)) & \text{otherwise}
\end{cases}
\]

(6)

where \( \text{diff}_k(t) \) is the average \( \text{diff}_k(t) \) value (a value exceeding 3.0 signifies a whisker deflection), and \( \sigma_i^{\text{fire}} \) is a unit-specific firing threshold (Table II).

The output \( s_i \) is calculated using

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**TABLE II**

Neuronal unit parameters for Darwin IX.

<table>
<thead>
<tr>
<th>Area</th>
<th>Size</th>
<th>( \sigma_i^{\text{fire}} )</th>
<th>( \omega )</th>
<th>( g )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Th</td>
<td>1x20</td>
<td>0.3</td>
<td>0.8</td>
<td>-</td>
</tr>
<tr>
<td>S1</td>
<td>1x20</td>
<td>0.1</td>
<td>0.0</td>
<td>1.0</td>
</tr>
<tr>
<td>S2</td>
<td>1x1</td>
<td>-0.10</td>
<td>0.6</td>
<td>1.0</td>
</tr>
<tr>
<td>Amy</td>
<td>1x1</td>
<td>0.0</td>
<td>0.0</td>
<td>1.75</td>
</tr>
<tr>
<td>Mave</td>
<td>3x6</td>
<td>0.0</td>
<td>0.0</td>
<td>1.0</td>
</tr>
<tr>
<td>FS</td>
<td>1x1</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

---

Fig. 3. Global neuroanatomy of Darwin IX. See text for details. Inset. The operation of two idealized lag cells (A and B). The post-stimulus internal state of cell A \( s_1(t) \) rises quickly (red dashed line), at a rate determined by \( \varphi_A \). The internal state of B \( s_2(t) \) rises more slowly (black dashed line, \( \varphi_B \)). When the internal state of each cell reaches a threshold \( \sigma_i^{\text{fire}} \), output is generated (solid lines) which decays at a rate determined by \( \omega \).

(B) subregions, such that each subregion receives input from a single whisker in the column on the corresponding side.

A global diagram of Darwin IX’s simulated nervous system is given in Fig. 3. It comprises 17 areas, 1101 neuronal units (see Table II), and ~8400 synaptic connections (see Table III). Neuronal units in area \( Th \) respond to whisker input with unit-specific time delays (see section D. Whisker input and lag cells). These units project topographically to the corresponding units of \( S1 \). Each subregion of \( S1 \) has local inhibitory connections which serve to increase the activity contrast among neuronal units. All subregions in \( S1 \) project to area \( S2 \) such that each neuronal unit in \( S2 \) takes input from 3 neuronal units, each of which is in a different subregion of either the left sub-area or the right sub-area of \( S1 \). This arrangement ensures that synaptic input to a neuronal unit in \( S2 \) is sparse and balanced. A deflection of a particular sequence of Darwin IX’s whiskers leads to a spatiotemporal pattern of activity in \( S2 \). Such a dynamic sequence is comparable to that observed in the rat brain [7].

Darwin IX’s nervous system also contains areas supporting the acquisition of conditioned aversion (see section G. Aversive conditioning). Area \( FS \) is activated by detection of a ‘foot-shock’ (see section H. Experimental environment and protocol), and projects to areas \( Amy, Mave \) and \( S \). Area \( Amy \) is analogous to the amygdala, a neural area which has been widely implicated in the acquisition of conditioned fear [12]. Area \( Mave \) is analogous to a motor cortical area, activity in which elicits an innate aversive freezing/escape response.

Activity in the simulated value system, area \( S \), signals the occurrence of salient sensory events and this activity contributes to the modulation of plastic connection strengths in the pathways \( S2 \rightarrow Amy \). Initially, \( S \) is activated by detection of simulated ‘foot-shock’. Activity in \( S \) is analogous to that
TABLE III
PROPERTIES OF ANATOMICAL PROJECTIONS IN DARWIN IX1.

<table>
<thead>
<tr>
<th>Projection</th>
<th>Arbor</th>
<th>P'</th>
<th>( c_{ij}(0) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( T_h \rightarrow S_1 )</td>
<td>[0x0]</td>
<td>1.0</td>
<td>13.0,15.0</td>
</tr>
<tr>
<td>( S_1 \rightarrow S_1(\text{intra}) )</td>
<td>[2x8]</td>
<td>1.0</td>
<td>-0.45,-0.6</td>
</tr>
<tr>
<td>( S_1 \rightarrow S_2 )</td>
<td>special</td>
<td>0.25,0.25</td>
<td></td>
</tr>
<tr>
<td>( FS \rightarrow Amy )</td>
<td>non-topo</td>
<td>1.0</td>
<td>5.0,5.0</td>
</tr>
<tr>
<td>( Amy \rightarrow M_{ave} )</td>
<td>non-topo</td>
<td>1.0</td>
<td>40.0,40.0</td>
</tr>
<tr>
<td>( FS \rightarrow M_{ave} )</td>
<td>non-topo</td>
<td>1.0</td>
<td>50.0,50.0</td>
</tr>
<tr>
<td>( FS \rightarrow S )</td>
<td>non-topo</td>
<td>1.0</td>
<td>50.0,50.0</td>
</tr>
<tr>
<td>( Amy \rightarrow S )</td>
<td>non-topo</td>
<td>1.0</td>
<td>-50.0,-50.0</td>
</tr>
<tr>
<td>( S_2 \rightarrow Amy )</td>
<td>non-topo</td>
<td>1.0</td>
<td>0.0001,0.0003</td>
</tr>
</tbody>
</table>

where \( \omega_i \) determines the persistence of unit activity from one cycle to the next (Table II). This value is fed as input into neuronal units in the corresponding subregions of \( S_1 \).

E. Neuronal dynamics

With the exception of the lag cells in area \( T_h \), the state of each neuronal unit in Darwin IX is determined by a mean firing rate variable \( s \), which corresponds to the average activity of a group of roughly 100 real neurons over 100 milliseconds (the ‘output’ of a lag cell \( s_k(t) \) is equivalent to the mean firing rate of neuronal units in other areas).

The mean firing rate \( \langle s \rangle \) of each neuronal unit ranges from 0 (quiescent) to 1 (maximal firing). For all neuronal units, except those in areas \( T_h \) and \( FS \), the total contribution of input to unit \( i \) is given by

\[
A_i(t) = \sum_{l}^{M} \sum_{j=1}^{NI} c_{ij}s_j(t) \tag{8}
\]

where \( M \) is the number of different anatomically defined connection types and \( NI \) is the number of connections per type \( M \) projecting to unit \( i \) (see Table III). The activity level of unit \( i \) is given by

\[
s_i(t+1) = \phi(\tanh(g_i(A_i(t) + \omega s_i(t)))) \tag{9}
\]

where \( \phi(x) = 0 \) for \( x < \sigma_i^{\text{fire}} \), otherwise \( \phi(x) = x \), \( g_i \) is a scale factor, and \( \omega \) determines the persistence of unit activity (Table II).

F. Synaptic plasticity

Synaptic plasticity in Darwin IX acts to strengthen connections between simultaneously active neuronal units in areas \( S_2 \) and \( Amy \). This process is ‘value dependent’, i.e. the degree of change is modulated by activity in the simulated value system (area \( S \)) according to the following rule:

\[
\Delta c_{ij}(t+1) = \eta s_j(t) BCM(s_i(t))(V(t) - 0.1) \tag{10}
\]

where \( \eta \) is a fixed learning rate (\( \eta = 1.4 \)), \( s_i(t) \) and \( s_j(t) \) are the activities of the post- and pre-synaptic units respectively and \( V(t) \) is the mean activity in area \( S \). The term \( (V(t) - 0.1) \) causes depression of plastic connections in the absence of value system activity.

The function \( BCM() \) is based on the rule of Bienenstock et al. [2] and is implemented as follows (\( \rho = 6, \theta_1 = \theta_2 = 0.1, k_1 = k_2 = 0.45 \)):

\[
BCM(x) = \begin{cases} 
0 & x < \theta_1 \\
k_1(\theta_1 - x) & \theta_1 \leq x < \theta_2 \\
k_2(\tanh(\rho(x - \theta_2))) & x < \theta_2 \\
\rho & \text{otherwise}
\end{cases} \tag{11}
\]

G. Aversive conditioning

Synaptic plasticity supports conditioned aversion to texture as follows. Area \( S \) maintains a baseline level of activity (0.1) in the absence of input \( (\sigma_i^{\text{fire}} = -0.1 \), see Table II). Detection of a simulated foot-shock (see section H. Experimental environment and protocol) causes neuronal units in area \( FS \) to produce a steady output of magnitude 1.0. This output pushes activity in area \( S \) above baseline, which causes potentiation of synapses onto neuronal units in area \( Amy \) from units in \( S_2 \) corresponding to the currently present texture (see equations (10,11)). Freezing/escape responses are triggered by activity in \( M_{ave} \) exceeding a threshold (0.5) as a result of input from areas \( FS \) and/or \( Amy \) (see Fig. 3). This model also supports extinction of conditioned responses: If \( Amy \) is activated without any corresponding foot-shock, area \( S \) will be inhibited such that its firing rate falls below baseline, and currently active synapses between \( Amy \) and \( S_2 \) will be weakened (see equations (10,11)).

H. Experimental environment and protocol

Fig. 4 shows the overall arrangement of Darwin IX’s environment. One texture (\( T_1 \)) consists of a vertically aligned column of pegs, the other (\( T_2 \)) consists of a vertically staggered set of pegs with offsets of \( \sim 6 \text{cm} \) (see Fig. 2B). Two adjacent walls contained \( T_1 \), the other two contained \( T_2 \), and either \( T_1 \) or \( T_2 \) can be associated with a simulated aversive foot-shock. Note that Darwin IX typically travels in both clockwise and anticlockwise directions around the environment such that the textures deflect both the left and right whisker arrays. Moreover, in the case of \( T_2 \), the pattern of whisker deflection depends on the direction of travel.

Experiments were divided into training and testing stages. During training, either \( T_1 \) or \( T_2 \) was paired with foot-shock and Darwin IX autonomously explored its enclosure for 25,000 cycles, corresponding to \( \sim 48 \) encounters with each wall and \( \sim 24 \) aversive responses to the simulated foot-shock. During
testing, the foot-shock pads were removed and Darwin IX was allowed to explore its enclosure for 15,000 cycles. Training and testing were repeated using three Darwin IX “subjects” initialized with different random seeds, and pairing both $T1$ and $T2$ with foot-shocks (six training/testing episodes in total). During training and testing of each subject, responses of all neuronal units were recorded and saved for analysis. The position of Darwin IX was also continuously recorded by an overhead camera that detected an array of LEDs positioned on the top surface of the robotic device, the images from which were time-stamped for analysis.

### III. Results

Texture discrimination by Darwin IX subjects was assessed by monitoring trajectories during testing. Fig. 5 shows the behavior of a single Darwin IX subject during training in which foot-shock was paired with $T1$, and during testing, in which the foot-shock pads were removed. Most aversive responses were in regions associated with the aversive texture.

Taking into account data from all subjects reveals near perfect conditioned avoidance of aversive textures. During testing, Darwin IX subjects which were trained to avoid $T1$ made aversive responses on 96.6% (S.E. = 0.18%) of encounters with $T1$. When trained to avoid $T2$, these subjects made aversive responses on 97.9% (S.E. = 0.14%) of encounters with $T2$ during testing. Only 3.2% of all aversive responses during testing occurred inappropriately, i.e. in response to whisker deflections by walls or by the texture not associated with foot-shock.

Darwin IX’s ability to categorize textural stimuli is supported by spatiotemporal patterns of activity in neural area $S2$. Each texture deflects whiskers in a column in a specific temporal order. The lag cells in area $Th$ and neural units downstream in $S1$ (see Fig. 3) present a pattern of activity with both a spatial component (i.e. the particular whisker) and a temporal component (i.e. the time since deflection). $S2$ responds to particular combinations of this $S1$ activity.

The population response of $S2$ to a texture was specific and repeatable. Fig. 6 shows representative $S2$ activity patterns during testing of a Darwin IX subject. The top panels show $S2$ activity during encounters of the left whisker column with texture $T1$. The bottom panels show encounters of the same whiskers with texture $T2$. While all panels show complex spatiotemporal patterns of activity, the top panels are highly similar to each other, the bottom panels are also highly similar to each other, but the top and bottom panels are dissimilar. This observation is supported quantitatively by measures of pattern similarity over time for all possible pairs, calculated as the normalized vector product (see Fig. 7). As shown in this figure, there is high similarity between activity patterns
Observations of Darwin IX show that time-lagged neuronal responses to somatosensory input together with value-dependent synaptic plasticity provide a plausible mechanism for the spatiotemporal transformations of sensory input needed for texture discrimination. This mechanism can provide a basis for selective conditioned aversion to textures.

Distinguishing among textures using only the information provided by whiskers involves multiple spatiotemporal transformations. The spatial patterns of textures are transformed, by self-movement, into temporal patterns of whisker deflections, which are themselves transformed into spatiotemporal patterns of neural activity in area S2, via a combination of the intrinsic properties of lag cells in area Th and the arrangement of projections in the pathway Th → S1 → S2.

As a result, neuronal units in S2 respond to specific combinations of whisker deflections with particular post-stimulus delays. Analysis of neural activity in S2 revealed the formation of spatiotemporal activity patterns corresponding to specific haptic perceptual categories (Fig. 6). The response properties of these units are analogous to cells with complex spatiotemporal receptive fields that have been found in rat somatosensory cortex [7] as well as in cat visual cortex [4].

Texture discrimination by Darwin IX was assessed behaviorally by a paradigm based on fear conditioning in which one texture was paired with a simulated foot-shock. In this paradigm, simulated foot-shock triggers a freezing/avoidance response and activates a value system which modulates synaptic plasticity between S2 and a neural area analogous to the rodent amygdala (Amyg). Activity in Amyg evokes a conditioned freezing and avoidance response via excitatory projections to M_{ ave}. As a result of these interactions, Darwin IX became conditioned to avoid theaversive texture.

Previous work on whisker-based perception in autonomous robots has focused either on texture discrimination by a fixed whisker array [6, 10, 14], or on obstacle avoidance by a mobile robot [3, 9]. Darwin IX extends these studies by showing texture discrimination using whisker arrays mounted on a behaving device, and by incorporating a neural simulation based on the rat somatosensory system. Our approach illustrates a very general mechanism for implementing spatiotemporal transformations that may underlie whisker-based perception in a variety of behavioral tasks.

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