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# Dynamic Remapping

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## 5 Introduction

6 The term *dynamic remapping* has been used in many different  
7 ways, but one of the clearest formulations of this concept comes  
8 from the mental rotation studies by Georgopoulos et al. (1989) (see  
9 also REACHING: CODING IN MOTOR CORTEX). In these experiments  
10 monkeys were trained to move a joystick in the direction of a visual  
11 stimulus or 90° counterclockwise from it. The brightness of the  
12 stimulus indicated which movement was required on a particular  
13 trial; a dim light corresponded to a 90° movement and a bright light  
14 to a direct movement. An analysis of reaction time suggested that,  
15 by default, the initial motor command always pointed straight at  
16 the target and then continuously rotated if the cue indicated a 90°  
17 rotation, an interpretation that was subsequently confirmed by single  
18 unit recordings.

19 The term *remapping* is also commonly used whenever a sensory  
20 input in one modality is transformed to a sensory representation in  
21 another modality. The best-known example in primates is the re-  
22 mapping of auditory space, from head-centered in the early stages  
23 of auditory processing to the retinotopic coordinates used in the  
24 superior colliculus (Jay and Sparks, 1987). This type of remapping,  
25 equivalent to a change of coordinates, is closely related to senso-  
26 rimotor transformations. It does not have to be performed over time  
27 but could be accomplished by the neuronal circuitry connecting  
28 different representations.

29 This review is divided into three parts. In the first part, we briefly  
30 describe the types of cortical representations typically encountered  
31 in dynamic remapping. We then summarize the results from several  
32 physiological studies where it has been possible to characterize the  
33 responses of neurons involved in temporal and spatial remappings.  
34 Finally, in the third part, we review modeling efforts to account for  
35 these processes.

## 36 Neural Representation of Vectors

37 A saccadic eye movement toward an object in space can be rep-  
38 resented as a vector  $\mathbf{S}$  whose components  $S_x$  and  $S_y$  correspond to  
39 the horizontal and vertical displacement of the eyes. Any sensory,  
40 or motor, variable can be represented by a similar vector. There are  
41 two major ways of representing a vector in a neural population—  
42 by a topographic map and by a nontopographic vectorial  
43 representation.

44 The encoding of saccadic eye movements in the superior collic-  
45 ulus is an example of a topographic map representation. A saccade  
46 is specified by the activity of a two-dimensional layer of neurons  
47 organized as a Euclidean manifold (see COLLICULAR VISUOMOTOR  
48 TRANSFORMATIONS FOR SACCADES). Before a saccade, a bump of  
49 activity appears on the map at a location corresponding to the hor-  
50 izontal and vertical displacement of the saccade.

51 Another example of a vectorial code is the code for the direction  
52 of hand movements in the primate motor cortex. Neurons in the  
53 primary motor cortex respond maximally for a particular direction  
54 of hand movement with a cosine tuning curve around this preferred  
55 direction (Georgopoulos et al., 1989). This suggests that each cell  
56 encodes the projection of the vector along its preferred direction.  
57 [Todorov (2000) questions this interpretation, but the precise iden-  
58 tity of the vector being encoded in motor cortex is not critical to  
59 the issue of remapping.]

60 In both cases, the original vector can be recovered from the popu-  
61 lation activity pattern using statistical estimators. Various examples  
62 of such estimators are described in DECODING POPULATION CODES.

## 63 Neurophysiological Correlates of Remapping

64 *Continuous Remappings*

65 Georgopoulos et al. (1989) studied how the population vector varies  
66 over time in the mental rotation experiment described in the  
67 introduction. They found that for movement 90° counterclockwise  
68 from the target, the vector encoded in M1 initially pointed in the  
69 target direction and then continuously rotated 90° counterclock-  
70 wise, at which point the monkey initiated a hand movement (Figure  
71 1A). This is consistent with the interpretation of the reaction time  
72 experiments: The monkey had initially planned to move toward the  
73 stimulus, and then updated this command according to the task  
74 requirement.

75 Similar continuous remapping occurs in the postsubiculum of  
76 the rat, one of the cortical structures involved in navigation of  
77 space. Neurons in the postsubiculum provide an internal compass  
78 that encodes the direction of the head with respect to remembered  
79 visual landmarks. The neurons have bell-shaped tuning curves  
80 around their best direction, similar to the code for hand direction  
81 in the primary motor cortex. Electrophysiological recordings have  
82 revealed that this vector is continuously updated as the head of the  
83 rat moves in space, even in complete darkness, suggesting that  
84 vestibular inputs are used for this updating (see RODENT HEAD  
85 DIRECTION SYSTEM).

86 Another example of continuous remappings has been reported  
87 in a double saccade task. In these experiments, two targets are  
88 briefly flashed in succession on the screen and the monkey makes  
89 successive saccades to their remembered locations (Figure 1B).  
90 Monkeys can perform this task with great accuracy, demonstrating  
91 that they do not simply keep a trace of the retinotopic location of  
92 the second target, since after the first eye movement this signal no  
93 longer corresponds to where the target was in space. Single unit  
94 recordings in the superior colliculus, frontal eye field, and parietal  
95 cortex have shown that the brain encodes the retinotopic location  
96 of the second target before the first saccade occurs. Then while the  
97 first eye movement is executed, this information is updated to rep-  
98 resent where the second target would appear on the retina after the  
99 first saccade (Figure 1C; Mays and Sparks, 1980). In certain cases,  
100 this update is predictive; i.e., it starts prior to the eye movement  
101 (Duhamel, Colby, and Goldsmith, 1992).

102 Graziano, Hu, and Gross (1997) have reported that the same  
103 mechanism appears to be at work in the premotor cortex. Bimodal,  
104 visuo-tactile neurons with receptive fields on the face remap the  
105 position of remembered visual stimuli after head movements. It is  
106 therefore becoming increasingly clear that continuous remappings  
107 are widespread throughout the brain and play a critical role in sen-  
108 sorimotor transformations.

109 Although all these examples clearly involve vector remappings,  
110 it is not entirely clear that the remappings are continuous. Hence,  
111 in the Georgopoulos et al. (1989) experiment, the population vector  
112 rotation could be a consequence of the simultaneous decay and  
113 growth of the initial planned hand direction and the final one, re-  
114 spectively, without ever activating intermediate directions. This is  
115 an example of one-shot remapping considered in the next section.  
116 Moreover, it is often difficult to determine whether a remapping in  
117 one particular area is computed in that area or is simply the reflec-  
118 tion of a remapping in an upstream area.

### 119 *One-Shot Sensory Remapping*

120 In the inferior colliculus and primary auditory cortex, neurons have  
121 bell-shaped auditory receptive fields in space whose positions are  
122 fixed with respect to the head. In contrast, in the multisensory layer  
123 of the superior colliculus, the positions of the auditory receptive  
124 fields are fixed in retinotopic coordinates, which implies that the  
125 auditory map must be combined with eye position (Jay and Sparks,  
126 1987). Therefore, the auditory space is remapped in visual coordi-  
127 nates, presumably for the purpose of allowing auditory targets to  
128 be foveated by saccadic eye movements, a function mediated by  
129 the superior colliculus.

130 A similar transformation has been found in the striatum and the  
131 premotor cortex, where some of the cells have visual receptive  
132 fields in somatosensory coordinates (skin-centered; Graziano et al.,  
133 1997). In all cases, these remappings are thought to reflect an in-  
134 termediate stage of processing in sensorimotor transformations.

135 These remappings can be considered as a change of coordinates,  
136 which correspond to a translation operation. For example, the au-  
137 ditory remapping in the superior colliculus requires the retinal lo-  
138 cation of the auditory stimulus,  $\mathbf{R}$ , which, to a first approximation,  
139 can be computed by subtracting its head-centered location,  $\mathbf{A}$ , from  
140 the current eye position,  $\mathbf{E}$ :

$$141 \quad \mathbf{R} = \mathbf{A} - \mathbf{E} \quad (1)$$

### 143 **Remapping Models**

144 The remappings we have described so far fall into two categories:  
145 vector rotation with a vectorial code (e.g., mental rotation) and  
146 vector translation within a topographic map (e.g., auditory remap-  
147 ping in the superior colliculus). These transformations are similar,  
148 since rotating a vector within a vectorial representation consists of  
149 translating a pattern of activity around a circle. Therefore, in both  
150 cases the remapping involves translating a bell-shaped pattern of  
151 activity across a map. Most models perform this operation either  
152 dynamically through time or in one shot through the hidden layer  
153 of a feedforward network (Figure 2).

#### 154 *Dynamical Models*

155 Two kinds of mechanisms have been used in models of continuous  
156 remapping: the integration of a velocity signal or the relaxation of  
157 a recurrent network.

159 *Integrative model for remapping.* In the double saccade paradigm  
160 described above, the retinal coordinates of the second target were  
161 updated during the first saccade, a process that might involve mov-  
162 ing a hill of activity within the parietal cortex. A model by Droulez  
163 and Berthoz (1991) shows how this bump of activity could be  
164 moved continuously across the map by integrating the eye veloc-  
165 ities during the first saccade (Figure 1A). Their model is essentially  
166 a *forward* model of motion: Given a velocity signal, it generates  
167 the corresponding moving image. Interestingly, the equations are  
168 similar to those used for *inverse* models of motion processing. In  
169 both cases, the analysis relies on the assumption that the temporal  
170 derivative of a moving image is zero. In other words, the overall  
171 gray level profile in the image is unchanged; only the positions of  
172 the image features change. It is possible to design a recurrent net-  
173 work to implement this constraint (Droulez and Berthoz, 1991),  
174 and the resulting network moves arbitrary patterns of activity in  
175 response to an instantaneous velocity signal.

176 Several variations of this idea have been developed. Dominey  
177 and Arbib have shown that an approximation of eye velocity, ob-  
178 tained from the eye position modulated neurons found in the pa-  
179 rietal cortex (see GAZE CODING IN THE POSTERIOR PARIETAL COR-  
180 TEX), is sufficient for this architecture to work (Dominey and Arbib,  
181 1992). Their simulations show patterns of activation very similar  
182 to the ones shown in Figure 1B in the part of their model corre-  
183 sponding to the parietal cortex, FEF, and superior colliculus. Zhang  
184 (1996) has used line attractor networks to model head direction  
185 cells in the postsubiculum of the rat. In this model, the hill is moved  
186 by using the velocity signal—in this case a head velocity signal—  
187 to temporarily modify the efficacy of the lateral connections.

189 *Recurrent networks.* Mental rotation of a population vector can  
190 be reproduced by training a neural network to follow a circular  
191 trajectory over time. In this case, the population vector rotates as  
192 a consequence of the network dynamics in the absence of any input  
193 signals. This approach has been used by Lukashin and Georgopou-  
194 los (1994) to model the generation of hand trajectories, but when  
195 the trajectory is a circle, mental rotation and a circular hand trajec-  
196 tory are equivalent. Although the model generates a rotating vector,  
197 additional mechanisms must be specified to stop the rotation.

#### 198 *Single-Shot Models*

199 Feedforward models have been used for vectorial as well as map  
200 representations. They are used whenever the amplitude of the shift  
201 is available to the brain beforehand, such as auditory remapping in

202 the superior colliculus in which the shift is directly proportional to  
203 the current eye position (Eq. 1). In contrast, for mental rotation,  
204 the amplitude of the shift is specified by an external stimulus.

206 *Shifter models.* As demonstrated by Touretzky, Redish, and Wan  
207 (1993), rotation within a vectorial representation can be performed  
208 by using a shifter circuit (for more details on shifter circuits, see  
209 ROUTING NETWORKS IN VISUAL CORTEX). Their architecture uses  
210  $N$  independent circuits, each implementing a rotation through a  
211 particular angle. This mechanism is limited in resolution since it  
212 rotates only by multiples of  $360/N$  degrees. Whether such shifter  
213 circuits actually exist in the brain remains to be demonstrated.

215 *Feedforward network models.* There are many examples of three-  
216 layer networks, and variations thereof, that have been trained or  
217 handcrafted to perform sensory remappings. Since these remap-  
218 pings perform vector addition, it might appear unnecessary to de-  
219 ploy a fully nonlinear network for such a task. However, with a  
220 map representation, vector addition requires moving a hill of ac-  
221 tivity in a map as illustrated in Figure 2B, an operation that is highly  
222 nonlinear.

223 Special-purpose nonlinear circuits can be designed to perform  
224 this operation (Groh and Sparks, 1992), but more biologically re-  
225 alistic solutions have been found with networks of sigmoidal units  
226 trained with backpropagation. Hence, the model of Zipser and An-  
227 dersen (see GAZE CODING IN THE POSTERIOR PARIETAL CORTEX),  
228 which was trained to compute a head-centered map from a retin-  
229 otopic input, uses hidden units with retinotopic receptive fields  
230 modulated by eye position, as in parietal neurons (see also Krom-  
231 menhoek et al., 1993).

232 However, backpropagation networks are generally quite difficult  
233 to analyze, providing realistic models but little insight into the al-  
234 gorithm used by the network. Pouget and Sejnowski (2001) have  
235 explored a way to analyze such networks using the theory of basis  
236 functions.

238 *Basis functions.* The process of moving a hill of activity in a  
239 single shot can be better understood when considered within the  
240 larger framework of nonlinear function approximation. For exam-  
241 ple, consider the feedforward network shown in Figure 2B, applied  
242 to a remapping from retinotopic,  $R_x$ , to head-centered coordinates,  
243  $A_x$ . Because of the map format used in the output later, the re-  
244 sponses of the output units are nonlinear in the input variables,  
245 namely, the retinal position,  $R_x$ , and eye position,  $E_x$ .

246 Therefore, the actual goal of the network is to find an appropriate  
247 intermediate representation to approximate this output function.  
248 One possibility is to use basis functions of  $R_x$  and  $E_x$  in the hidden  
249 layer (Pouget and Sejnowski, 2001; Salinas and Abbot, 1995).

250 Perhaps the best-known set of basis functions is the set of cosine  
251 and sine functions used in the Fourier transform. Another example  
252 is the set of Gaussian or radially symmetric functions with local  
253 support (see RADIAL BASIS FUNCTION NETWORKS). A good model  
254 of the response of parietal neurons, which are believed to be in-  
255 volved in remapping, is a set of Gaussian functions of retinal po-  
256 sition multiplied by sigmoid functions of eye position. The result-  
257 ing response function is very similar to that of gain-modulated  
258 neurons in the posterior parietal cortex [see GAZE CODING IN THE  
259 POSTERIOR PARIETAL CORTEX, and Pouget and Snyder (2000) for  
260 a review].

## 261 Conclusions

262 Remappings can be continuous and dynamic or a single shot  
263 through several layers of neurons. In both cases, the problem  
264 amounts to moving a hill of activity in neuronal maps. Whether  
265 some models are better than others is often difficult to establish  
266 simply because the neurophysiological data available are relatively  
267 sparse. Models can be further constrained by considering deficits  
268 that accompany localized lesions in humans (see Pouget and Se-  
269 jnowski, 2001). These data not only provide valuable insights into  
270 the nature of remappings but also might help bridge the gap be-  
271 tween behavior and single cell responses.

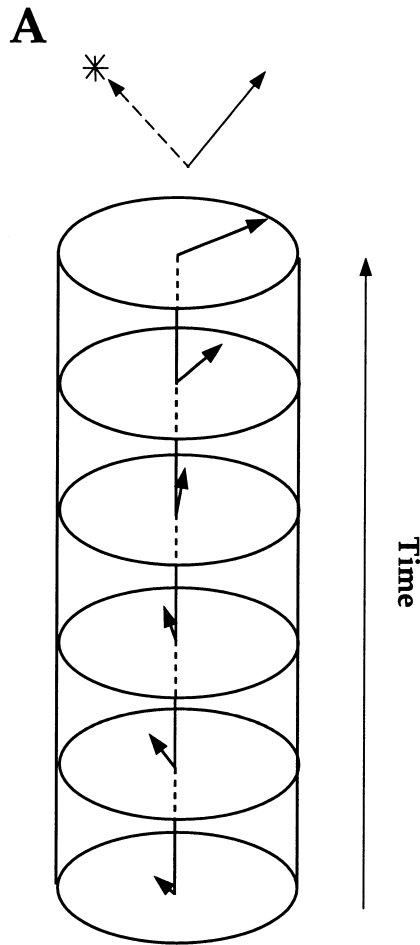
272 **Roadmap:** Vision  
273 **Related Reading:** Collicular Visuomotor Transformations for Saccades;  
274 Motion Perception, Elementary Mechanisms; Pursuit Eye Movements;  
275 Visual Attention; Visual Scene Perception, Neurophysiology

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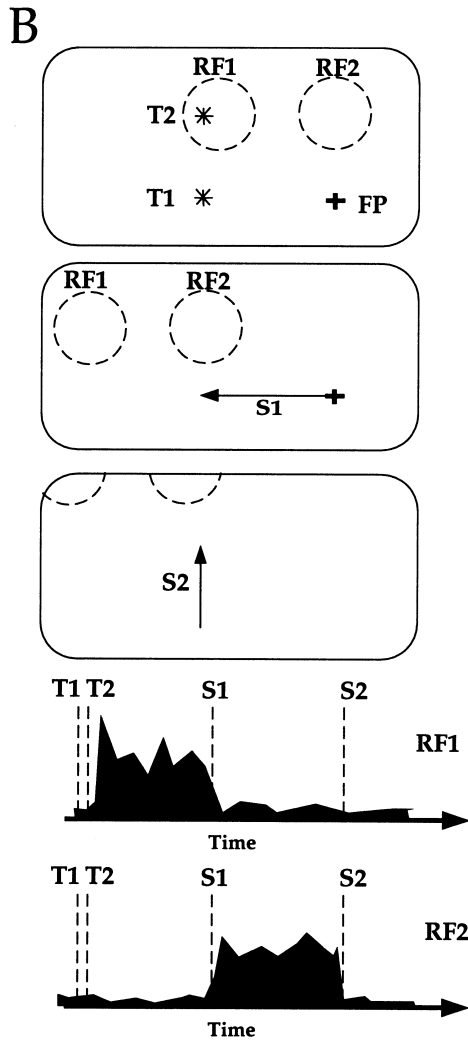
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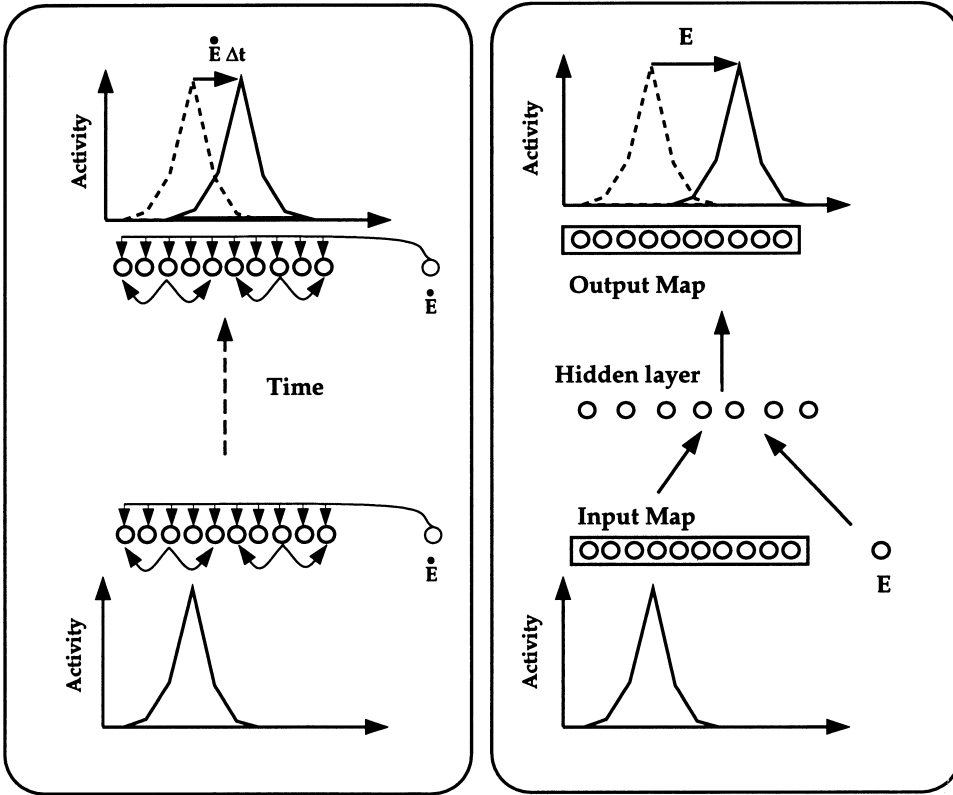


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**Figure 1.** A, Rotation of population vector in the primary motor cortex when the brightness of the target (star) indicates a 90° clockwise movement. (Adapted from Georgopoulos et al., 1989.) B, Saccade remapping. The monkey makes a double saccade (S1 and S2) to the remembered positions of T1 and T2. C, Post-stimulus-time histograms showing the responses of two cells with receptive fields RF1 and RF2 illustrated in Figure 1B. The second cell (RF2) responds only after the first eye movement, encoding the new retinal location of T2, even though it is no longer present on the screen.

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**Figure 2.** In a map representation, remappings involve moving hills of activity. These hills can be moved continuously in a recurrent network (A), or in one shot in a feedforward network (B). A, The recurrent network dynamically moves the hill of activity according to a velocity signal,  $\dot{E}$ . As described in the text, there are several ways to achieve this result. Droulez and Berthoz (1991) integrate the eye velocity signals through the lateral connections while Zhang (1996) uses the eye velocity signals to temporally bias the lateral connections. B, In feedforward remapping, the hill is moved in one shot by the full amount of the current displacement,  $E$ , via an intermediate stage of processing in the hidden layer. The weights can be adjusted with a learning algorithm such as backpropagation. Alternatively, one can use basis function units in the hidden layer and train the weights to the output units with a simple learning algorithm such as the delta rule.