

## Integrating computation into the mechanistic hierarchy in the cognitive and neural sciences

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**Abstract:** It is generally accepted that, in the cognitive sciences, there are both computational and mechanistic explanations. We ask how computational explanations can integrate into the mechanistic hierarchy. The problem stems from the fact that implementation and mechanistic relations have different forms. The implementation relation, from the states of an abstract computational system (e.g., an automaton) to the physical, implementing states is a homomorphism mapping relation. The mechanistic relation, however, is that of part/whole; the explanans in a mechanistic explanation are components of the explanandum phenomenon. Moreover, each component in one level of mechanism is constituted and explained by components of an underlying level of mechanism. Hence, it seems, computational variables and functions cannot be mechanistically explained by the medium-dependent properties that implement them. How then, do the computational and implementational properties integrate to create the mechanistic hierarchy? After explicating the general problem (section 2), we further demonstrate it through a concrete example, of reinforcement learning, in cognitive neuroscience (sections 3 and 4). We then examine two possible solutions (section 5). On one solution, the mechanistic hierarchy embeds at the same levels computational and implementational properties. This picture fits with the view that computational explanations are mechanism sketches. On the other solution, there are two separate hierarchies, one computational and another implementational, which are related by the implementation relation. This picture fits with the view that computational explanations are functional and autonomous explanations. It is less clear how these solutions fit with the view that computational explanations are full-fledged mechanistic explanations. Finally, we argue that both pictures are consistent with the reinforcement learning example, but that scientific practice does not align with the view that computational models are merely mechanistic sketches (section 6).

## 1 **1. Introduction**

2 The question of how different explanations in the cognitive sciences relate to each  
3 other is widely debated (Kaplan and Craver, 2011; Piccinini and Craver, 2011;  
4 Piccinini, 2015; Shapiro, 2017). We focus here on the relations between mechanistic  
5 explanations and computational explanations in the neuro-cognitive sciences.  
6 Mechanistic models describe the phenomenon's underlying mechanism. Often, they  
7 are considered explanatory because they describe a relevant causal structure,  
8 namely, the causal structure that underlies the explanandum. Moreover, there is a  
9 hierarchy of mechanistic explanations - each component in a mechanistic  
10 explanation is itself explained mechanistically. Computational explanations are  
11 similar to mathematical explanations in that they describe phenomena in abstract –  
12 mathematical or formal – terms. Computational explanations, however, are abstract  
13 in a further sense. They arguably describe abstract, “medium-independent”,  
14 features. Thus, in computational explanations both the describing terms and the  
15 described objects/properties are abstract.

16 Several authors have recently suggested that computational explanations are a  
17 species of mechanistic explanation (Kaplan, 2011; Kaplan and Craver, 2011; Piccinini  
18 and Craver, 2011; Milkowski, 2013; Piccinini, 2015; Boone and Piccinini, 2016; Coelho  
19 Mollo, 2018; Dewhurst, 2018). The focus of most of these accounts is the neuro-  
20 cognitive sciences, in which computational models and explanations are central to  
21 the scientific investigation. Though the accounts are different in detail, they all share  
22 the starting point that computational explanations are in some sense abstract,  
23 whereas mechanistic explanations describe causal relations between physical  
24 entities. Each account offers a unique way to bridge the apparent disparity between  
25 computational and mechanistic explanations.

26 Whether computational models are indeed mechanistic is still under controversy  
27 (Huneman, 2010; Piccinini and Craver, 2011; Weiskopf, 2011; Kaplan, 2011; Kaplan  
28 and Craver, 2011; Lange, 2013; Chirimuuta, 2014, 2018; Bechtel and Shagrir, 2015;  
29 Rathkopf, 2015; Craver, 2016; Shagrir and Bechtel, 2017; Shapiro, 2017; Craver and  
30 Povich, 2017; Egan, 2017). Here we do not focus on this controversy (though our

31 analysis might have some implications regarding the nature of computation). Our  
32 concern is with the integration of computation – mechanistic or not – within the  
33 hierarchy of mechanistic explanations. The concern arises from the disparity  
34 between the implementation (or realization) relation and the explanans-  
35 explanandum relation in mechanistic explanations. The implementation relation  
36 from the states of an abstract computational system (e.g., an automaton) to the  
37 states of its implementing physical system is a homomorphism mapping relation, so  
38 that each distinct computational state is mapped onto a distinct physical state, which  
39 realizes it. The mechanistic relation, however, is that of part/whole. The explanans in  
40 a mechanistic explanation are components of the explanandum phenomenon.  
41 Moreover, each component in one level of mechanism is constituted and explained  
42 by components of another, underlying, level of mechanism. Hence, it seems,  
43 computational states are realized in some physical structures, but they do not stand  
44 in part/whole relations to them and therefore they cannot be mechanistically  
45 explained by the same structures. So, the question is: how do computational states  
46 integrate with implementational states to form the mechanistic hierarchy?

47 Before turning to address this question, we want to describe the main features of  
48 mechanistic and computational explanations. Mechanistic explanations have three  
49 main features: they are causal, decompositional and hierarchical. They are causal in  
50 that they explain phenomena by describing their underlying mechanism. Consider  
51 the reflex that is responsible for keeping the direction of gaze constant when the  
52 head is rotated horizontally. It is called the horizontal vestibulo-ocular reflex. Its  
53 function is explained by reference to an underlying mechanism whose inputs are the  
54 effects of head movements on the vestibular organ and whose outputs are given to  
55 the ocular muscles. Within the mechanism there are feedforward inhibitory and  
56 excitatory synaptic connections, so that each pre-synaptic neuron causally affects  
57 the post-synaptic neurons through the synaptic connections (Kandel *et al.*, 2013,  
58 chap. 40). Mechanistic explanations are decompositional because the explanandum  
59 phenomenon is explained in terms of its components, their organization and their  
60 activities (functions). In our example the constant gaze when the head is rotated is  
61 explained by appeal to the specific synaptic connections between neurons, as well as

62 the neurons' change in firing rate in response to their synaptic inputs. Finally,  
63 mechanistic explanations are hierarchical: each explaining component in one level is  
64 itself the explanandum for another level of mechanism. Accordingly, the release of  
65 neurotransmitter to the synapse by the pre-synaptic neuron, is also explained  
66 mechanistically (see (Piccinini and Craver, 2011)). Our focus here is the third feature  
67 of mechanistic explanations, namely, the mechanistic hierarchy. An important point  
68 about the hierarchy is that each level in the hierarchy is a mechanistic explanation.

69 Computational explanations are taken to be abstract in that they refer to abstract,  
70 "medium-independent", properties. This claim is fairly uncontroversial.<sup>1</sup> What  
71 perhaps is more controversial is the claim that computational explanations refer *only*  
72 to abstract, formal properties. Some authors argue that computational explanations  
73 also refer to semantic properties, namely to the specific content of the states  
74 (Shagrir, 2006; Sprevak, 2010); others might insist that computational explanations  
75 also refer to some implementational, medium-dependent, properties (Some of the  
76 writings of (Kaplan, 2011, 2017; Dewhurst, 2018) may be interpreted this way). We  
77 will not get into the debate about the nature of physical computation. Our concern is  
78 with the integration of abstract states and properties of computation in the  
79 mechanistic hierarchy<sup>2</sup>. We take abstract here to mean 'medium-independent' in the  
80 sense that they can be implemented in very different physical media (e.g., both in  
81 brains and in computers). We will refer to these states and properties as  
82 computational. But by this we assume in no way that computational states and  
83 processes are only abstract.

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<sup>1</sup> There are, however, different ways to account for the nature of these "medium-independent" properties. Fodor (1975) and Stich (1983) describe them as "syntactic" properties, and Fodor (1994) accounts for the latter in terms of high-level physical properties. Haugeland (1981) describes them as "formal" (see also (Fodor, 1980)). Piccinini (2015) describes computational properties as "mathematical" or "formal", and others have suggested that, regarding computations, the relevant physical properties of the implementing physical systems are only their degrees of freedom (Piccinini and Bahar, 2013; Coelho Mollo, 2018).

<sup>2</sup> While it seems straightforward to associate the computational explanations discussed here with Marr's computational level (1982), algorithmic descriptions of a system can also be abstract and computational in the meaning we discuss here, as long as they are 'medium-independent'. These algorithmic descriptions are more similar to mechanistic explanations in that they usually decompose the explanandum into its parts, while computational level explanations describe 'what' function the system performs and 'why' (Shagrir and Bechtel, 2017).

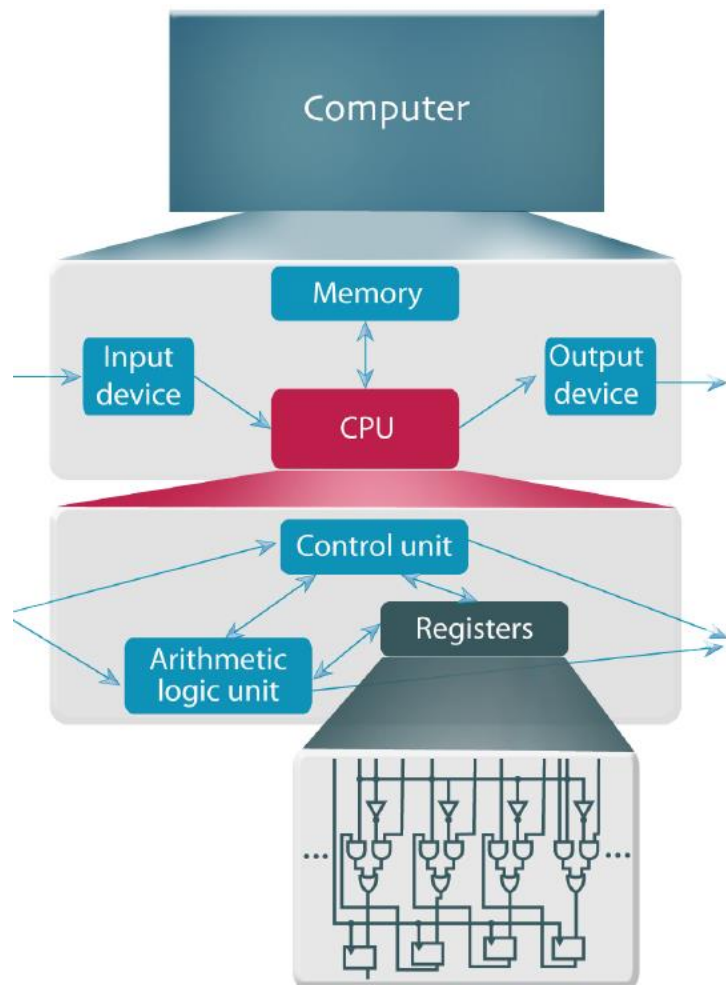
## 85 **2. The computational and implementational hierarchies**

86 Let us turn to the problem of integrating computational states and properties within  
87 the mechanistic hierarchy. As a warm-up, let us look at the way Piccinini describes  
88 this integration. Piccinini (2015), who defends the view that computational  
89 explanations are mechanistic, takes those computational levels to be levels of  
90 mechanism. In a crucial paragraph in his book he says the following:

91       The mechanistic account flows naturally from these theses. Computing  
92       systems, such as calculators and computers, consist of component parts  
93       (processors, memory units, input devices, and output devices), their function  
94       and organization. Those components also consist of component parts (e.g.,  
95       registers and circuits), their function, and their organization. Those, in turn,  
96       consist of primitive computing components (paradigmatically, logic gates),  
97       their functions, and their organization. Primitive computing components can  
98       be further analyzed mechanistically but not computationally (2015, pp. 118–  
99       119).

100 Now, we think that it is uncontroversial that Piccinini describes here levels of  
101 computation that relate to each other in a part/whole relation. As Piccinini depicts it,  
102 computers consist of processors, memory etc., which in turn consist of registers and  
103 circuits, which in turn consist of logic gates (figure 1).

104 Figure 1 – The computational hierarchy



105

106 However, Piccinini does make a controversial claim, namely that computational  
 107 explanations are mechanistic. This claim has been criticized on three main grounds.  
 108 Some critics argue that, even if some computational explanations are  
 109 decompositional as in the described case, there are other cases in which  
 110 computational explanations do not decompose the explananda into components,  
 111 but instead refer to general structural or topological properties of the system, and so  
 112 are not mechanistic (Huneman, 2010; Rathkopf, 2015; but see Craver, 2016). A  
 113 second criticism is that computational explanations do not always aim to reveal  
 114 causal structures. Egan (2017) suggests that computational models are explanatory  
 115 because they are abstract and normative. Chirimuuta (2014) suggests that some  
 116 computational models explain why a computation takes place by appeal to efficient  
 117 coding principles, and Shagrir and Bechtel suggest that some computational models  
 118 also explain the existence of a computation by appeal to environmental constraints

119 (Bechtel and Shagrir, 2015; Shagrir and Bechtel, 2017). According to these two  
120 criticisms, computational explanations are not wholly mechanistic, but it still may be  
121 that some computational explanations, which refer to medium-independent  
122 properties, are decompositional, and therefore may be mechanistic.

123 Other critics argue that, even when computational explanations involve  
124 decomposition, the resulting levels of computation are not levels of mechanisms.  
125 Instead, they argue that these levels are functional; they are part of a functional  
126 analysis which explains the capacity (Fodor, 1968; Cummins, 1983, 2000). These  
127 critics would agree that the levels are decompositional, relating to each other in a  
128 part/whole fashion, which is perfectly consistent with the functional account of  
129 computational explanations. They would also agree that the pertinent computational  
130 properties are "medium-independent", at least in the sense that they refer to  
131 abstract and not to medium-dependent, implementational, properties. The critics  
132 would argue, however, that the divide between the abstract/medium-independent  
133 properties and implementational properties is indicative of the divide between  
134 functional and mechanistic explanations (Weiskopf, 2011; Shapiro, 2017). Because  
135 functional and implementational entities are inherently different, computational and  
136 mechanistic explanations take place in different levels of explanation. Piccinini  
137 (2015) in turn rejects the functional/mechanistic distinction, arguing that functional  
138 explanations are sketches of mechanism (Piccinini and Craver, 2011). Moreover, he  
139 argues that computational explanations are (ideally) both abstract and full-fledged  
140 mechanistic. They are abstract in the sense that they refer to medium-independent  
141 properties. They are mechanistic in the sense that the medium-independent  
142 properties constrain the implementation ((Piccinini, 2015) But see Shapiro (2017) for  
143 criticism).

144 We put aside the question of whether the computational level – as a level of  
145 abstract, medium-independent, properties – sufficiently constrains implementation  
146 to be considered mechanistic. We want to highlight a different issue that Piccinini  
147 and others do not discuss, namely, the way that computational (medium-  
148 independent) and implementational (medium-dependent) properties relate to each  
149 other in the mechanistic hierarchy.

150 The picture depicted by Piccinini raises two (related) issues. The first pertains to the  
151 primitive computing components. Piccinini says that “primitive computing  
152 components can be further analyzed mechanistically but not computationally”. He  
153 means that we can further analyze the logic gates in terms of non-computational,  
154 medium-dependent properties. The difficulty is that the logic gates are also  
155 *implemented* in some medium-dependent properties. The inputs and outputs of  
156 logic gates – typically characterized as 1s and 0s – are often implemented in systems  
157 with specific voltages. The implementing physical objects with specific voltages,  
158 however, are not *parts* of the digits. More generally, implementation is often  
159 characterized as a mapping homomorphism relation from the states of an abstract  
160 computing system (e.g., an automaton) to groups of states of a physical system. For  
161 example, there is a mapping from the digits 0 and 1 to the sets of voltages, 0-5 volts  
162 and 5-10 volts. The sets of voltages, however, are not themselves the mechanism  
163 that constitute the digits. The question raised, then, is about the relations between  
164 the medium-independent properties that analyze computation in the mechanistic  
165 explanation and the medium-dependent properties that implement computation.  
166 The first ones, the analyzing properties, seem to be parts of the digits, whereas the  
167 second ones, the implementing properties, are not. Are these the same properties  
168 and how do they relate to each other? We expect a part-whole mechanistic analysis,  
169 but we can only find in this stage an implementation-relation and not a part-whole  
170 relation, so how can logic gates be explained mechanistically?

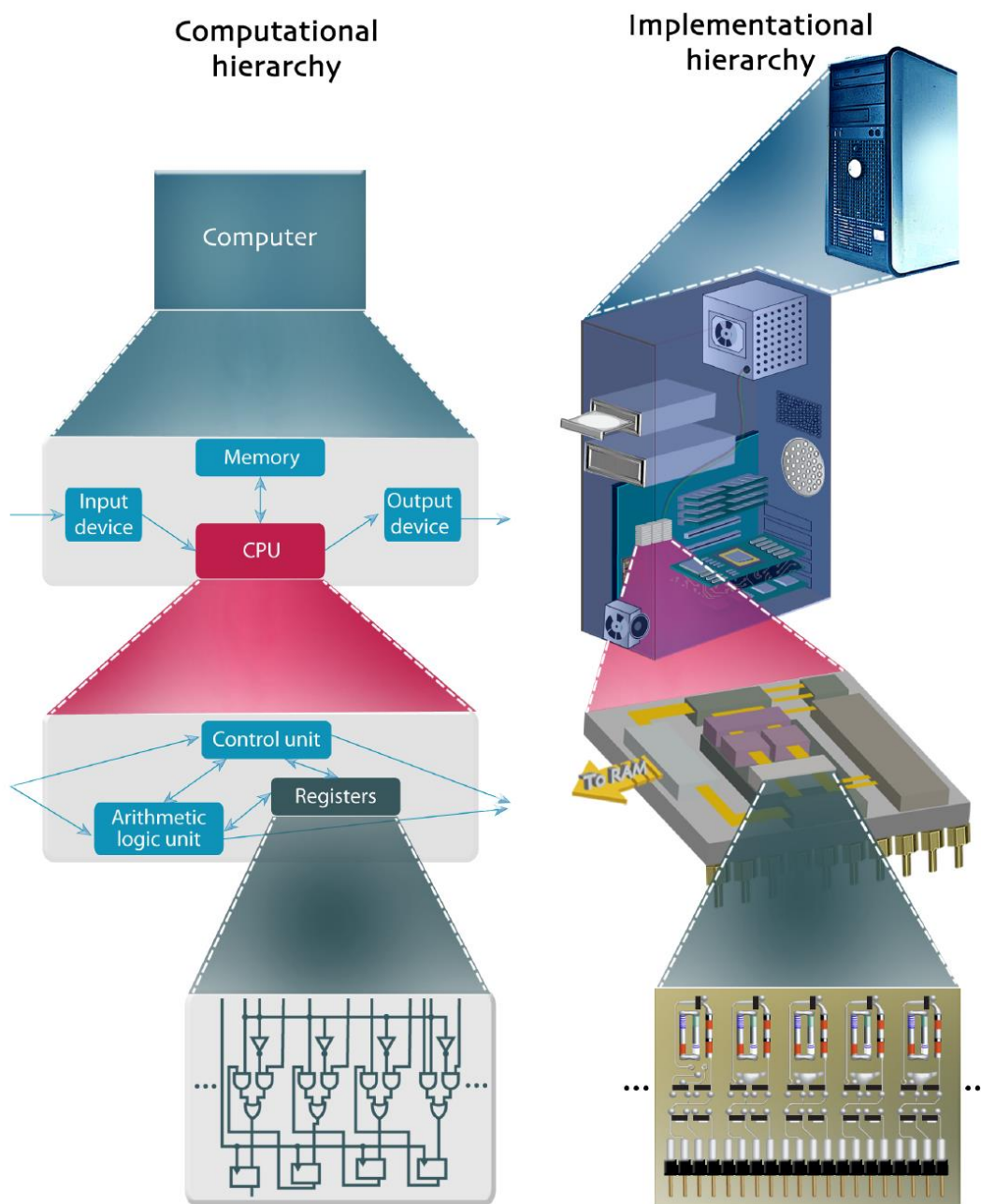
171 A second issue concerns the non-primitive computing components. The components  
172 of a higher-level computation are analyzed by an underlying computational level. But  
173 they are also implemented in some medium-dependent properties. How are these  
174 underlying properties – the computational and implementational – related? Take the  
175 computational level that consists of “component parts (e.g., registers and circuits),  
176 their function, and their organization”. Let us call it  $C_n$ . The components of  $C_n$  can be  
177 analyzed, computationally, by the computational components of an underlying  
178 computational level  $C_{n-1}$  (e.g., logic gates). However, the computational components  
179 of  $C_n$  are also implemented in some medium-dependent properties that belong to  
180 some mechanistic level,  $P_k$ . But how are  $P_k$  and  $C_{n-1}$  related in the mechanistic



181 hierarchy? Moreover,  $P_k$  itself is part of a hierarchy,  $P_0, P_1, P_2, \dots$ . So, there are two  
182 hierarchies, one computational,  $C_1, C_2, \dots$  and one implementational,  $P_0, P_1, P_2, \dots$   
183 (figure 2).

184

185 Figure 2 The computational and implementational hierarchies



186

187 Several issues are worthwhile addressing regarding this picture. First, in some cases  
188 computational explanations are not decompositional (Huneman, 2010; Chirimuuta,  
189 2014; Bechtel and Shagrir, 2015; Rathkopf, 2015; Egan, 2017; Shagrir and Bechtel,  
190 2017), and therefore are not hierarchical. Although in such cases we will not find two  
191 or more hierarchies, the question of how the single-level computational explanation  
192 is integrated into the implementational hierarchy persists.

193 We would also like to note that much of the structure of these two hierarchies and  
194 their relations depends on how one defines ‘a level of explanation’. There is  
195 practically unanimous agreement that in the scientific investigation of cognitive  
196 capacities both the underlying computation and the underlying implementation  
197 should be addressed eventually. The question that is under debate addresses the  
198 relevant details for a complete explanation of a capacity at a specific level. According  
199 to the mechanistic framework, a complete explanation at each level will include all  
200 the causally relevant relations and activities that constitute the explanandum  
201 capacity.

202 Our question then is how the computational, medium-independent properties and  
203 their implementational, medium-dependent, properties relate to each other in the  
204 scientific explanation.<sup>3</sup> Do we really find two hierarchies, one computational and one  
205 implementational, in which each level in each hierarchy is a complete explanation?  
206 And if this is indeed the case, then how do the two hierarchies relate to each other?

### 207 **3. A hierarchical computational model for reinforcement learning**

208 It could be argued that the two hierarchies we describe in the decomposition of the  
209 computer are the result of a specific man-made design, and that the observations  
210 from a computer cannot be generalized to the cognitive sciences. For this reason, it

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<sup>3</sup> One can also ask how the implementational hierarchy is decomposed. Depending on one’s view of a level of explanation, the implementational hierarchy will include different details. It can include merely a reference to the physical structures that underlie the computational function. Alternatively, this hierarchy can also describe functions executed by these structures, albeit, medium-dependent functions. To illustrate, diodes, which are used on occasion to build logic gates in computers, have the function of passing electric current in exactly one direction. Description of such functions can be a part of the implementational hierarchy, because such functions are not abstract, but instead describe medium-dependent processes. In both cases the decomposition of the implementational hierarchy will depend on some function, in the first case it is the computational function, and in the second it is the medium-dependent function (which may or may not coincide with the computational function).

211 is useful to examine the relation between computation and implementation in the  
212 mechanistic hierarchy with the help of an example from neuro-cognitive science.

213 Reinforcement learning is a behavior in which the subject learns to choose specific  
214 actions according to their consequences, with the goal of maximizing rewards. It is  
215 widely investigated; it has received attention both from computer scientists who  
216 have suggested algorithms for action selection that maximize specific outcomes  
217 (Sutton and Barto, 1998), and from neural and cognitive scientists who have  
218 compared various reinforcement learning models with subjects' behaviors (Mongillo,  
219 Shteingart and Loewenstein, 2014; Shteingart and Loewenstein, 2014) and searched  
220 for neural correlates of variables from reinforcement learning algorithms (Samejima  
221 *et al.*, 2005; Li and Daw, 2011; Wang, Miura and Uchida, 2013).

222 Reinforcement learning is a process that requires multiple different computations,  
223 and as such it can be viewed hierarchically. At the highest level, reinforcement  
224 learning is divided into four main processes, each involving its own computations:  
225 recognizing the subject's state, evaluating potential actions, selecting an action, and  
226 reevaluating the action based on the outcome (Doya, 2008).

227 Each one of these processes has been discussed in large bodies of literature and can  
228 be further decomposed in various ways. To provide more concrete examples we will  
229 discuss reinforcement learning in the context of a multi-armed bandit task, where  
230 there is only one state in which the subject repeatedly chooses between multiple  
231 actions, each associated with a certain magnitude and probability of reward. We  
232 describe here a simple and widely used algorithm for reinforcement learning, which  
233 is called Q-learning (because the values associated with the actions are called Q-  
234 values) (Sutton and Barto, 1998). In a multi-armed bandit task, reinforcement  
235 learning has two main modules (instead of the four we originally mentioned), action  
236 reevaluation and action selection.

237 Consider the module which is responsible for reevaluating an action after an  
238 outcome. In Q-learning, each Q-value is meant to reflect the expected reward  
239 associated with each action, also called the action-value. In order to learn this  
240 action-value, after each trial a variable called the reward prediction error (RPE) is

241 computed. The RPE is the difference between the reward that was just received and  
242 the current value of the chosen action:

243 
$$\text{for the chosen action } a_i \rightarrow RPE(t) = R(t) - V_i(t) \quad (1)$$

244 Where  $R(t)$  is the reward given at time  $t$ ,  $a_i$  is action  $i$  and  $V_i(t)$  is the action-value  
245 of action  $i$  at time  $t$ . Then, the value of the chosen action is updated by summing the  
246 previous value with a magnitude that is proportional to the RPE. Written formally:

247 
$$\begin{aligned} \text{if } a_i \text{ was chosen} &\rightarrow V_i(t+1) = V_i(t) + \alpha \cdot RPE(t) \\ \text{if } a_i \text{ was not chosen} &\rightarrow V_i(t+1) = V_i(t) \end{aligned} \quad (2)$$

248 Where  $\alpha$  is a parameter that indicates the learning rate. The larger  $\alpha$  is, the more  
249 weight recent trials are given at the expense of previous trials.

250 If we wish, we can continue this hierarchical computational explanation, by  
251 explaining how the components in eq. (1)-(2) are computed. For example, we can  
252 explain how the learning rate ' $\alpha$ ' is computed. We can also explain how the reward is  
253 evaluated, or what the initial conditions set for  $V_i(t=0)$  are.

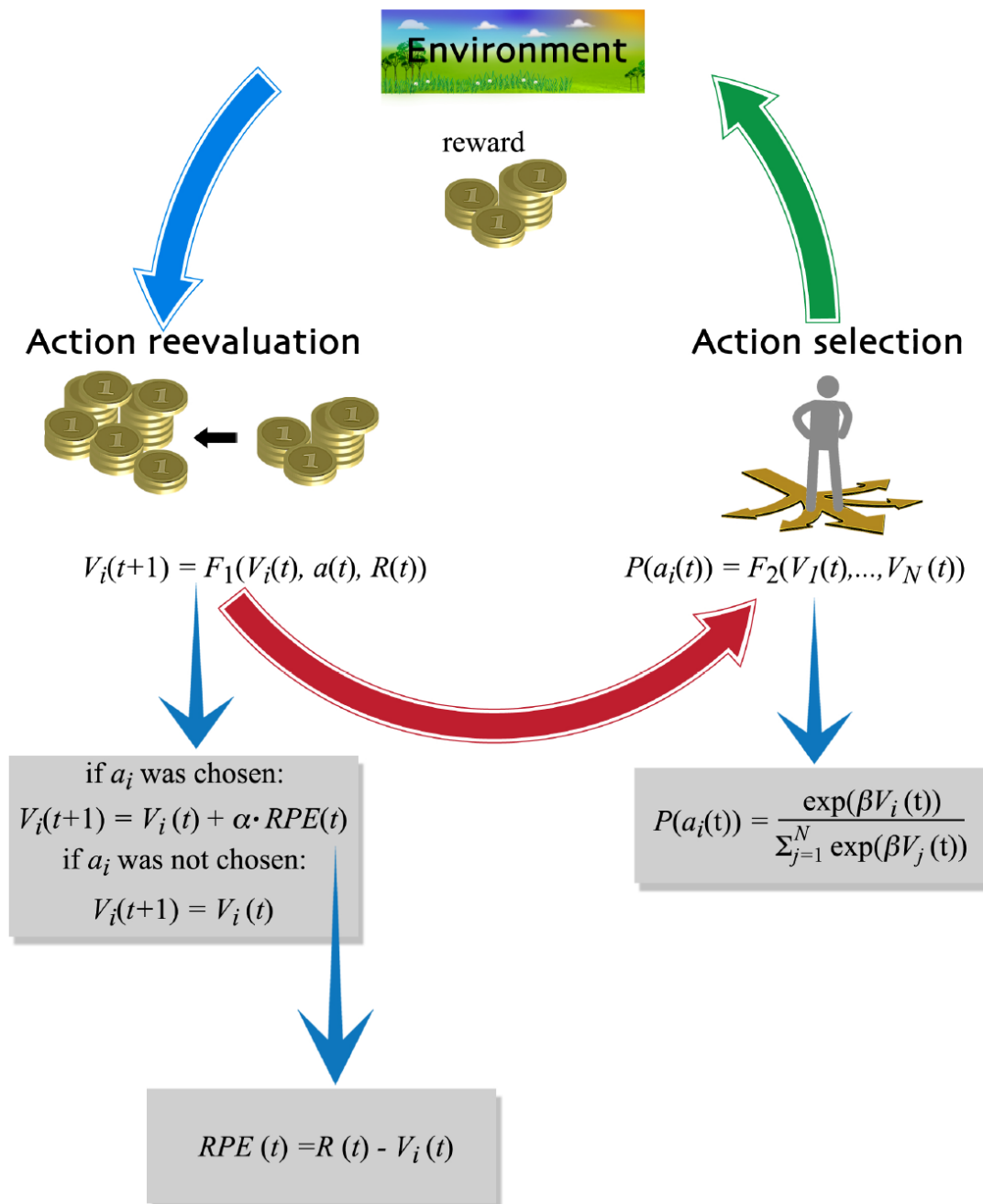
254 Consider now the second module, the module that is responsible for selecting  
255 between different actions. The simplest kind of module would just select the action  
256 that has the highest value, according to the computation in eq. (2). However, this  
257 method may never sample actions that initially received lower values, even in cases  
258 where these lower values were underestimates of the true values. Therefore, it is  
259 generally agreed that some form of exploration is required, i.e., actions with lower  
260 values should be chosen with a non-zero probability. A common model that  
261 incorporates exploration into the choice is a 'softmax' function where actions with  
262 higher values have a higher probability to be chosen. The 'softmax' function is:

263 
$$P(a_i(t)) = \frac{e^{\beta V_i(t)}}{\sum_{j=1}^n e^{\beta V_j(t)}} \quad (3)$$

264 Where  $a_i$  is action  $i$ ,  $P(a_i(t))$  is the probability of choosing action  $i$  at time  $t$ ,  $V_i(t)$   
265 is the action-value of action  $i$  at time  $t$ ,  $n$  is the number of possible actions, and  $\beta$  is  
266 a parameter that determines the bias of the choice towards the higher valued

267 actions. The components of this action selection function can also be further  
 268 explained. For example, in this equation, the choice is stochastic. We can also  
 269 provide a model for this stochasticity. Or we can explain the choice of  $\beta$ , which may  
 270 be a constant, or change throughout learning. Fig. 3 presents a summary of the  
 271 hierarchical model we described so far.

272 Figure 3 The computational hierarchy of the Q-learning model



274 Using the two modules described above, in a multi-armed bandit task, in which  
275 subjects choose between several actions repeatedly, it is possible to learn to choose  
276 the action that is associated with the largest expected reward most frequently.  
277 Hence, a popular theory in the cognitive sciences is that people employ a model  
278 similar to Q-learning in various instances of reinforcement learning tasks.

279 Q-learning is not the only model that has been suggested for reinforcement learning,  
280 it has a few competitors at several different levels. First, some reinforcement  
281 learning algorithms do not compute the values of actions at all. Instead, learning is  
282 done directly on the 'policy': the probability of choosing each action. These are  
283 called direct-policy learning algorithms (Mongillo, Shteingart and Loewenstein, 2014;  
284 Shteingart and Loewenstein, 2014). Second, in the Q-learning model the action  
285 selection function (eq. 3) utilizes the same action-values as the action reevaluation  
286 function (eq. 2). However, in some reinforcement learning algorithms, the action  
287 selection function does not employ the action-value estimates of the action  
288 reevaluation function. Instead, the only signal the action-selection function receives  
289 from the action-reevaluation function is the RPE. In these algorithms, these two  
290 modules are also called the 'actor' and the 'critic', respectively (Sutton and Barto,  
291 1998). A third issue concerns the complexity of Q-learning. It is argued that it is too  
292 simple to explain a wide variety of behaviors and therefore this original model has  
293 been developed into alternative, more complicated models (Botvinick, Niv and Barto,  
294 2009; Botvinick, 2012). Each of these three groups of competing models challenges a  
295 different part of the computational hierarchy of Q-learning. The first group of  
296 models challenges whether there is an action reevaluation function at all, the second  
297 group of models questions the relation between the action selection and the action  
298 reevaluation functions and the third presents alternatives to the structure within  
299 each function.

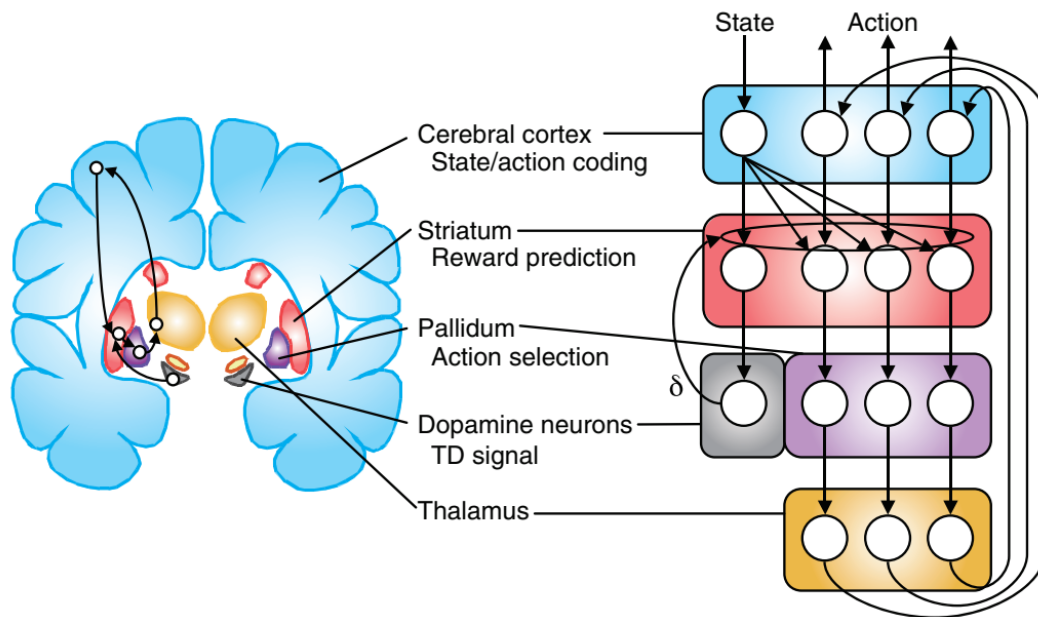
300 We believe that the point is clear, the Q-learning model is hierarchical in nature.  
301 Furthermore, all properties discussed in the Q-learning model are medium-  
302 independent: they do not necessitate a specific physical structure. In fact, they are  
303 abstract enough that they can be both implemented in computers and, as many

304 scientists hypothesize, in brains (Schultz, Dayan and Montague, 1997; Doya, 2000,  
305 2008; O'Doherty *et al.*, 2004; Samejima *et al.*, 2005).

#### 306 **4. The computational and implementational hierarchies of reinforcement learning**

307 A great deal of scientific research has been dedicated to the characterization of the  
308 neural correlates of the Q-learning model (Hollerman and Schultz, 1998; Doya, 2000,  
309 2008; Samejima *et al.*, 2005; Ito and Doya, 2009; Kable and Glimcher, 2009; Tai *et al.*,  
310 2012; Wang, Miura and Uchida, 2013). Experimental evidence has implicated the  
311 basal ganglia, a group of several subcortical nuclei, including the striatum, pallidum  
312 and substantia nigra, in decision making, and specifically in the context of  
313 reinforcement learning (Doya, 2000). With regard to the different modules of  
314 reinforcement learning, the coding of state and possible actions in each state has  
315 been attributed to the cortex, the calculation of the expected reward associated  
316 with each action (action reevaluation) has been attributed to the striatum, action  
317 selection has been attributed to the pallidum, etc. In Fig. 4 you can see a scientific  
318 hypothetical model which describes the implementation of the computational  
319 modules in reinforcement learning.

320 Figure 4. The implementational model for reinforcement learning. Adopted from  
321 (Doya, 2008). Legend is taken from the original paper.



**Figure 2** A hypothetical model of realization of reinforcement learning in the cortex–basal ganglia network<sup>2</sup>. Left, coronal section of the brain. Right, functional model, where  $\delta$  denotes the reward prediction error carried by the midbrain dopamine neurons.

322

323 The attribution of specific computational properties to brain areas corresponds to  
 324 their connectivity patterns. On the Q-learning model we expect action-values to play  
 325 a part in the action selection function (eq. 3). On our implementational model  
 326 striatal neurons represent action-values and pallidal neurons are responsible for  
 327 action selection. Indeed, in line with the computational model, we see that striatal  
 328 neurons target and causally affect pallidal neurons. Hence, on this description,  
 329 abstract computational relations are translated into causal relations between  
 330 physical brain areas.<sup>4</sup>

331 One can wonder about the model on the right-hand side of Fig. 4. While the model  
 332 on the left-hand side clearly describes causal relations between brain areas, the  
 333 model on the right-hand side is abstract and is termed functional by (Doya, 2008).  
 334 Although its drawing is abstract, this model is committed to specific brain areas,  
 335 sometimes describing brain areas without an apparent function (such as the  
 336 Thalamus). For this reason, it would be difficult to consider this model a functional  
 337 analysis, as described by (Fodor, 1968; Cummins, 1983, 2000). Furthermore, this

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<sup>4</sup> Some may argue that relations between computational components can already be considered causal relations. We discuss the possible outcomes of this position in section 5.



338 model is committed to specific media, namely, brain areas, and therefore it does not  
339 describe medium-independent properties. For this reason, we consider it an  
340 implementational model. However, for those who believe that computational  
341 models are both complete mechanistic explanations and medium-independent  
342 (Piccinini, 2015), this model, which focuses on the abstract functions of specific brain  
343 areas, may be similar to what they have in mind<sup>5</sup>.

344 The components in the implementation described in Fig. 4 can be decomposed  
345 themselves into subparts, which correspond to parts of the computations. For  
346 example, there is experimental evidence that midbrain dopaminergic neurons that  
347 provide input to striatal neurons, encode the reward prediction error (RPE) (eq. 1),  
348 which is a component in the calculation of action-values (eq. 2) (Schultz, Dayan and  
349 Montague, 1997; Hollerman and Schultz, 1998). To provide another example,  
350 neurons in both the ventral and dorsal striatum receive inputs from midbrain  
351 dopamine neurons, which are taken to encode the RPE (note the arrow from the  
352 gray box to the red box in Fig. 4). Therefore, both are taken to play a role in reward  
353 prediction. Experimental findings have suggested that neuronal activity in the  
354 striatum can be divided into two anatomically and functionally separate parts of  
355 reward prediction: the dorsal striatum plays a role in associating stimuli with  
356 responses, corresponding primarily to an ‘actor’ (action selection) module, while the  
357 ventral striatum plays a role in updating the predictions of future rewards expected  
358 in each state, corresponding to a ‘critic’ (action reevaluation) module (O’Doherty *et*  
359 *al.*, 2004).

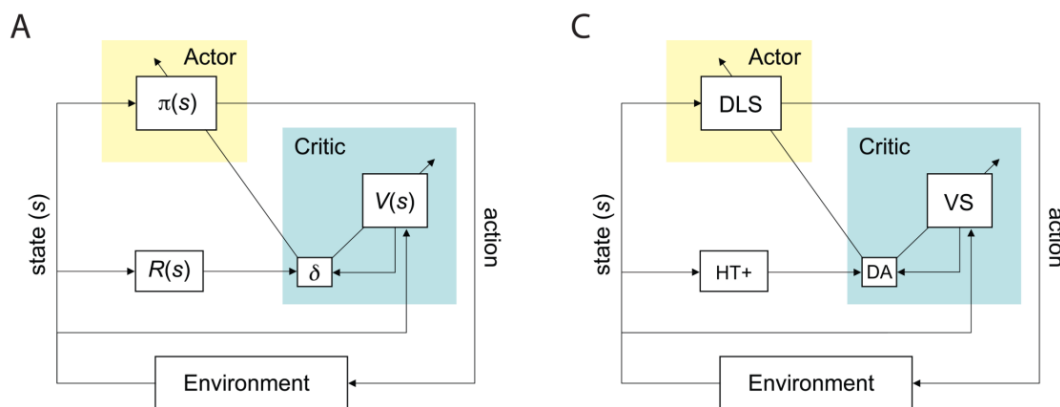
360 We see in this example two distinct hierarchies, one computational and one  
361 implementational. Parts of the computational hierarchy can be seen in Fig. 3. This  
362 hierarchy is abstract, medium-independent and can be discussed without mention of  
363 any brain structures. We can also see an implementational hierarchy, part of it is  
364 depicted in fig. 4, where brain structures are decomposed into functionally and  
365 anatomically individuated components. In some scientific publications we even see

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<sup>5</sup> If this is the case, some issues regarding this view should be resolved. Most importantly, how function can remain medium-independent when it is necessary to state the brain structure in which they occur (Haimovici, 2013).

366 computational and implementational models for decision making (albeit slightly  
367 different models from the Q-learning model) depicted side by side, as in Fig. 5.

368 Figure 5 Computational and implementational models, side by side. Adopted from  
369 (Botvinick, Niv and Barto, 2009).  $R(s)$ : reward function;  $V(s)$ : value function;  $\delta$ :  
370 reward prediction error;  $\pi(s)$ : policy (action-selection function). DA: dopamine; DLS,  
371 dorsolateral striatum; HT+: hypothalamus and other structures; VS, ventral striatum.



372

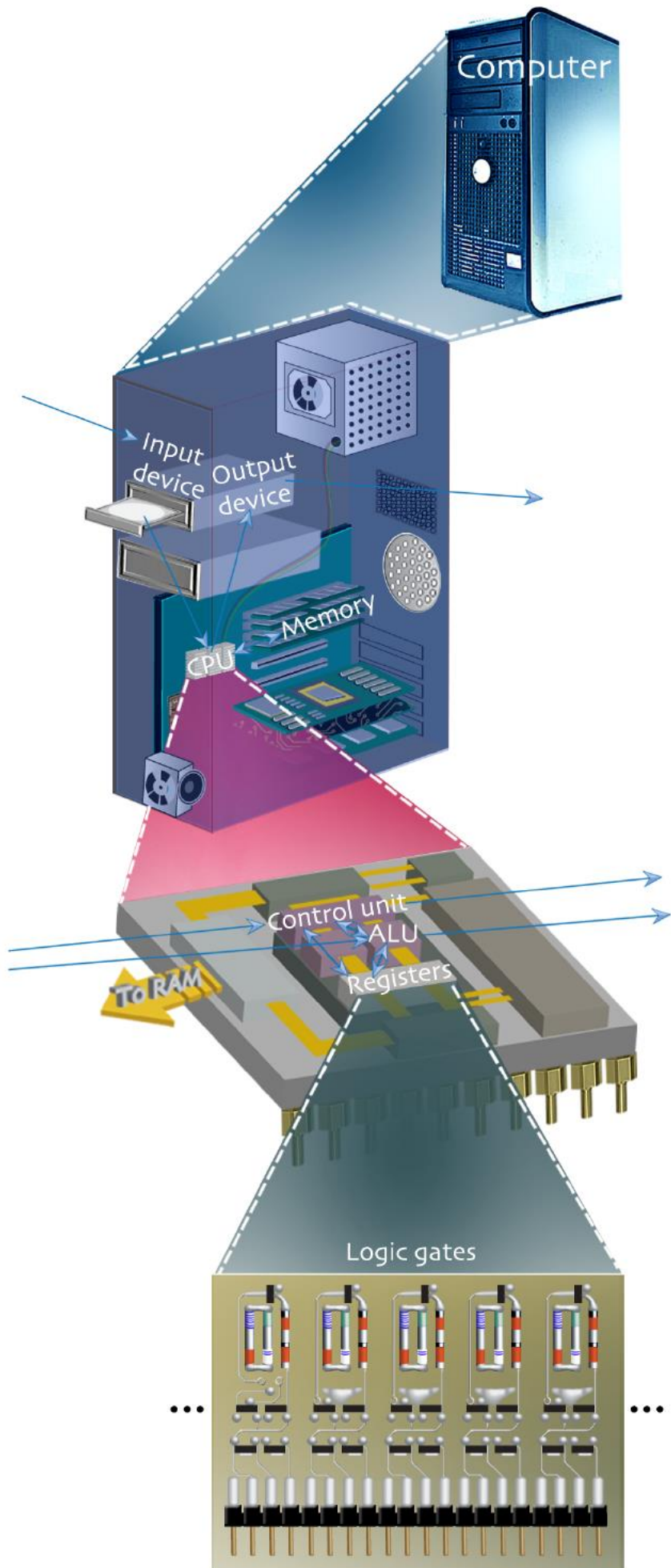
373 The relation between these two hierarchies is that of implementation, throughout  
374 the scientific literature brain structures are described as ‘implementing’ (Ito and  
375 Doya, 2011), ‘realizing’ (Doya, 2008), ‘representing’ (Samejima *et al.*, 2005) and  
376 ‘encoding’ (Schultz, Dayan and Montague, 1997) computational properties.

### 377 5. The relation between the computational and implementational hierarchies

378 We found in our scientific example two hierarchies, like the ones described in Fig. 2.  
379 However, there are still many open questions about these hierarchies, both in  
380 general and in our example. How do these hierarchies relate to each other within the  
381 scientific explanation? How does this relation reflect the explanatory role of the  
382 computational and implementational models? Finally, what role do implementation  
383 relations and part/whole relations play in the explanation of cognitive phenomena?  
384 In this section, we suggest possible answers to these questions and investigate their  
385 merit. We relate these possible answers to the different views about abstractness  
386 and completeness of computational models. We do not aim to support one stance  
387 on this question, but instead wish to examine the consequence of the different  
388 positions about computational models as explanations and start a debate about  
389 these possible solutions.

390 We can think of two ways to relate computation and implementation to each other  
391 within the mechanistic hierarchy. One is lumping together the implementational and  
392 the abstract properties in each level, namely C1 and P1, C2 and P2 and so on. Figure  
393 6 shows an example of this picture on the decomposition of a computer.

394 Figure 6 A single combined mechanistic hierarchy. Each level includes both abstract  
395 and implementational properties that are related through implementation. The  
396 implementational properties are denoted by the drawings in the figure, while the  
397 computational properties are denoted by the words and arrows appearing on top of  
398 the implementational properties.



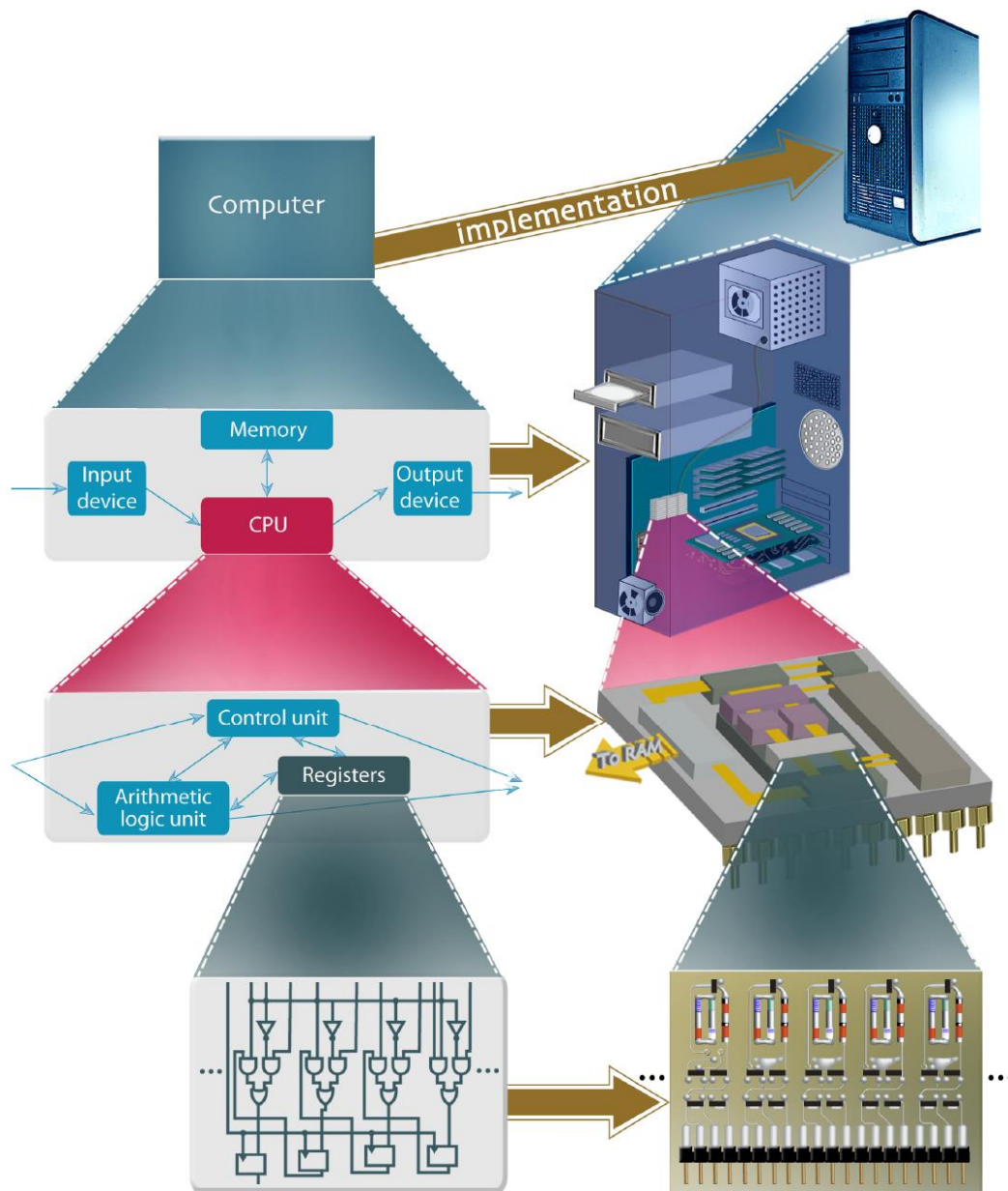
400 On this picture we do not really have two separate hierarchies, but only one: The  
401 pertinent computational properties are lumped together with their  
402 implementational properties in the same level(s) of explanation (a similar structure  
403 of explanation is presented in (Harbecke, under review)). This simple solution implies  
404 that computational and implementational properties figure together in the same  
405 explanation and in the same levels of the mechanistic hierarchy. This solution is in  
406 tension with the view that computational explanations are autonomous from  
407 implementation and therefore do not require implementation details to be  
408 complete, but fits quite nicely with the picture on which computational explanations  
409 are sketches of mechanisms (some people, e.g., (Rusanen and Lappi, 2016; Shagrir,  
410 2016) interpret (Kaplan and Craver, 2011; Piccinini and Craver, 2011) as advocates of  
411 this position). On this picture, the computational sketches turn into a full-fledged  
412 mechanistic explanation only when we complement the sketches with the same-  
413 level implementational properties. When both kinds of properties are mentioned  
414 then we have a full-fledged mechanistic explanation, hence a level of mechanism.  
415 The mechanistic hierarchy simply embeds within it, a sub-hierarchy of computational  
416 sketches.

417 We can see two possible upshots of this construal, depending on one's view of  
418 computational models as sketches. One may consider computational sketches to  
419 simply be partial descriptions of the implementational model and computational  
420 properties to simply be abstract facets of the implementing properties, stripped  
421 away from their medium-dependent aspects. On this formulation, when the  
422 implementing properties are described in an explanation, the computational  
423 properties, which are merely a part of the implementational properties, become  
424 redundant. We are left with an implementational hierarchy, partial descriptions of  
425 which are computational models. On such a view it is clear how there is only one  
426 mechanistic hierarchy – an implementational hierarchy. However, this view  
427 completely dismisses any explanatory value of computational descriptions that goes  
428 above implementational descriptions and some may argue that this is inconsistent  
429 with scientific practice, which often appeals to computational explanations as more  
430 than partial implementational descriptions (Haimovici, 2013). Alternatively, one may

431 believe that computational sketches can include details and aspects which are not  
432 part of the implementational model. For example, that they address environmental  
433 constraints or efficient coding principles (Chirimuuta, 2014; Bechtel and Shagrir,  
434 2015; Shagrir and Bechtel, 2017). Therefore, in the complete model both  
435 computational and implementational properties figure together. This view takes  
436 computational descriptions to be more than partial implementational descriptions,  
437 but it brings up the original problem discussed in this paper - how the unique  
438 computational properties relate to the implementational properties in each level of  
439 the hierarchy.

440 A second option is to keep the two hierarchies apart (figure 7). The two hierarchies  
441 are related through the implementation relation. The computational properties of  
442 C1 are mapped (implemented by) to the implementational properties of P1, the  
443 computational properties of C2 are mapped to the implementational properties of  
444 P2, and so on. While objects by the same name may appear in both hierarchies, such  
445 as CPUs and registers in Fig. 7, the computational hierarchy includes only abstract,  
446 medium-independent properties (e.g., digits in logic gates) and the implementational  
447 hierarchy includes physical, medium-dependent properties (e.g., voltages). Fig. 7  
448 presents a simple case where each computational level is mapped to each  
449 implementational level. In reality there might not be a perfect match between the  
450 hierarchies and computational properties at the same level may be implemented in  
451 implementational properties in different levels. However the structure of the  
452 implementation relation, in all cases in this picture there are two hierarchies and the  
453 computational properties in the computational hierarch are implemented by  
454 implementational properties in the implementational hierarchy. This solution is  
455 more hospitable to the notion that there is multiple realization of cognitive  
456 functions, since the same computational hierarchy can be related to (i.e.,  
457 implemented in) different implementational hierarchies.

458 Figure 7 Two separate hierarchies, one computational and one implementational,  
459 that are related through implementation. Each level in each hierarchy is a complete  
460 explanation of the phenomenon at the higher level.



461

462 This picture fits quite nicely with the functional view of explanation, namely, the idea  
 463 that computational explanations are full-fledged functional (yet non-mechanistic)  
 464 explanations. According to this functional picture, computational explanations are  
 465 distinct and autonomous from mechanistic explanations (Fodor, 1968; Cummins,  
 466 1983), which fits with the solution in which the two hierarchies are distinct.  
 467 Computational and implementational properties do not figure together in the  
 468 decompositional explanation of the same capacities. Instead, only computational  
 469 properties are part of the decomposition of computations. Implementational  
 470 properties can still figure in explanations of computations, but these explanations

471 will not be mechanistic because there is no part/whole relation between explanans  
472 and explanandum. While on this picture the two hierarchies are separate, they still  
473 constrain each other: the relevant implementational properties are determined  
474 according to the computational function, and the computational hierarchy must be  
475 one which can be implemented in the physical system. Despite these mutual  
476 constraints, those supporting this picture will argue that the computation performed  
477 as part of some cognitive capacity can be given a complete explanation at one level  
478 without any reference to implementation and that the implementation details  
479 explain a different aspect of this capacity, namely, how the capacity is implemented.  
480 That is, computational and implementational explanations answer different  
481 questions.

482 On both pictures, primitive computing processes are analyzed mechanistically, if at  
483 all, only indirectly. The primitive computational components, e.g., logic gates, are  
484 *implemented* in some implementational properties, e.g., voltages, whereas only the  
485 latter can be further analyzed mechanistically. On the combined-hierarchy picture  
486 (Fig. 6), the computational properties will figure together with implementational  
487 properties in each level, until at some point the primitive computing processes can  
488 no longer be decomposed, and only implementational properties will continue to be  
489 decomposed in the hierarchy. On the separate-hierarchies picture (Fig. 7), the  
490 computational hierarchy will terminate at the primitive computing components.

491 On both pictures, the implementation is not a part/whole relation and therefore the  
492 description of implementation cannot be taken as a mechanistic explanation.  
493 Nonetheless, these two pictures do differ in how they view the role of  
494 implementation in explanation in general. On the combined picture, both  
495 computational and implementational details figure together in one mechanistic  
496 hierarchy. Therefore, it is natural to take relations of implementation to not have an  
497 explanatory role. Instead, medium-dependent details are taken to explain by  
498 decomposition of the phenomena. On the separate-hierarchies picture  
499 implementation can be considered to have a non-mechanistic explanatory role: it  
500 explains how the explanandum, as well as the computational hierarchy are  
501 implemented (see (Coelho Mollo, 2018)).



502 What about the view that computational explanations are both abstract and full-  
503 fledged mechanistic explanations? It would be difficult to see how the first solution  
504 in Fig. 6 can be consistent with it; if computational explanations are complete  
505 mechanistic explanations why do they require additional implementation details in  
506 the same mechanistic level of explanation? The second solution in Fig. 7 is not  
507 necessarily inconsistent with this view. For example, if one takes computational  
508 states and properties to have causal powers, then one can view the computational  
509 hierarchy as a hierarchy of complete mechanistic explanations. However, on this  
510 view the role of the implementational hierarchy still needs to be explicated. A  
511 possible implication is that the overall mechanistic picture is more complex: We have  
512 different mechanistic hierarchies that apply to different properties of the same  
513 objects/components. But under this picture any computational capacity has at least  
514 two hierarchical explanations, and it is not obvious which one of them should be  
515 considered *the* mechanistic explanation. A possible way to elucidate this complex  
516 picture is to maintain that the implementational hierarchy explains how the  
517 computational hierarchy is implemented, rather than how the cognitive capacity is  
518 performed (Coelho Mollo, 2018). On this view, the computational hierarchy is the  
519 mechanistic hierarchy which decomposes the cognitive capacity and the  
520 implementational hierarchy is an appendix which explain the implementation of the  
521 computation.

## 522 **6. Some insights from reinforcement learning**

523 It can be useful to examine the relation between the hierarchies in reinforcement  
524 learning. When considering the computational and implementational hierarchical  
525 models for reinforcement learning, which solution best describes the relation  
526 between these hierarchies? We believe that evidence in this case is mixed and can  
527 support both suggested solutions for the relation between the hierarchies. On the  
528 picture seen on Fig. 6, each level combines computation and implementation into  
529 one mechanistic explanation. Therefore, we would expect the scientific investigation  
530 of lower levels to include a physical decomposition of the higher level, as occurs in  
531 mechanistic explanations. However, in our example the scientific investigation of the  
532 implementation of the computational hierarchy searches for the implementation of

533 variables at various levels of this hierarchy, such as the representations of action-  
534 value (Samejima *et al.*, 2005), RPE (Schultz, Dayan and Montague, 1997) and learning  
535 rate ( $\alpha$  in eq. 1) (Behrens *et al.*, 2007). Often, the search for a lower-level variable  
536 such as the learning rate takes place in the absence of a scientifically supported  
537 neural correlate for the higher level computational variable of which it consists (In  
538 this case the calculation of action-value). Hence, the search for neural correlates  
539 here is more akin to searching for relations between two separate computational  
540 and implementational hierarchies than to physically decomposing mechanisms.

541 Moreover, scientific investigation of both hierarchies can and has been conducted  
542 separately. The Q-learning algorithm for reinforcement learning has been  
543 investigated both analytically (Watkins and Dayan, 1992) and behaviorally  
544 (Shteingart, Neiman and Loewenstein, 2013). These methods ignore the neural  
545 correlates of this model. Similarly, the basal ganglia have been investigated  
546 anatomically and functionally without addressing computational models for  
547 reinforcement learning (Hoshi *et al.*, 2005). This suggests that a framework of two  
548 hierarchies, as presented in Fig. 7, is the appropriate one in this case.

549 On the other hand, it can be argued that current scientific research is still preliminary  
550 and not indicative of the final form of a fully-fledged scientific explanation. Hints that  
551 such a form will include one combined mechanistic hierarchy can be found in the  
552 fact that scientific debates today about the plausibility of specific computational  
553 models of reinforcement learning often also appeal to the plausibility of the  
554 implementation of these models (Botvinick, Niv and Barto, 2009).

555 Moreover, findings of implementation of specific computational variables can be  
556 used to support or refute abstract computational models. Recall the three challenges  
557 to the computational model we presented in the section 3. The first one suggested  
558 that instead of learning the values of the actions, there is 'direct-policy' learning  
559 where the probability of choosing each action (i.e., the policy) is reevaluated at each  
560 step. However, the finding that striatal neurons represent the expected reward  
561 associated with each action (Samejima *et al.*, 2005) can be taken as support for the

562 hypothesis that a Q-learning model is implemented in the brain, rather than a  
563 'direct-policy' model<sup>6</sup>.

564 The finding in (O'Doherty *et al.*, 2004) that striatal neurons can be divided into  
565 'actor' and 'critic' modules can be used as evidence in the second challenge:  
566 whether the action selection and action reevaluation modules can be separated into  
567 'actor' and 'critic'. It is also increasingly popular to suggest computational models  
568 that are informed by the structure of neural networks, with the purpose of  
569 suggesting models that are more biologically plausible (Mnih *et al.*, 2016). Note that,  
570 even though physical structures are used as evidence in this debate, the questions  
571 pertain to the architecture of the abstract computational model, which can be  
572 implemented both in computers and in brains.

573 Given these examples it can be argued that the practice of developing a complete  
574 explanation at each level of the explanatory hierarchy involves a close and reciprocal  
575 relation between the computational models and their possible implementation, and  
576 that computational models are not considered explanations until they have been  
577 shown to be implemented in the brain. This suggests that computation and  
578 implementation belong together in one level of the explanation. Therefore, the  
579 pictures presented in Figs. 6-7 are both still possible regarding this example.

580 However, when considering whether computational descriptions are merely  
581 sketches of mechanisms, on the interpretation of sketches as partial descriptions of  
582 implementation, the evidence is more conclusive. We see that, in our example of  
583 reinforcement learning, evidence from scientific practice is strongly against the view  
584 of computational models as sketches. Moreover, scientific practice tends to take  
585 implementational details to explain the implementation of the computational model  
586 rather than the cognitive capacity directly. Often, when findings of neural correlates  
587 of reinforcement learning models are reported, they are reported as discoveries  
588 about the implementation of these models. Hence, such findings are taken to  
589 answer questions about how, and whether a specific computational model is  
590 implemented in the brain and they do not attempt to explain reinforcement learning

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<sup>6</sup> But see (Elber-Dorozko and Loewenstein, 2018)

591 (or decision making in general) without appeal to some computational model.  
592 Perhaps the strongest indication for this is in experiments where there is some  
593 causal intervention on brain areas and behavioral changes are measured. If  
594 computational models are merely partial descriptions of implementation, they will  
595 be unnecessary in the interpretation of causal experiments, where the causal  
596 structure is already described in the results of the experiment. However, often,  
597 results in such experiments are interpreted in the framework of a computational  
598 model of reinforcement learning (Tai *et al.*, 2012; Wang, Miura and Uchida, 2013;  
599 Lee *et al.*, 2015). For example, (Tai *et al.*, 2012) find that stimulation of striatal  
600 neurons causes a bias in choices, and they interpret these results by saying that  
601 stimulation of striatal neurons mimics changes in action-value. Hence, instead of  
602 utilizing the causal finding to explain the behavior of the subjects, (Tai *et al.*, 2012)  
603 use their finding as an indication of implementation of action-value – a  
604 computational variable. Such a computational interpretation to causal results is  
605 difficult to explain if computational models are taken to be merely partial  
606 descriptions of causal mechanisms and is much more in line with the view that  
607 computational models have a unique explanatory value. Moreover, this scientific  
608 practice can be taken to support the claim that implementational details are taken to  
609 explain the computational model rather than the cognitive capacity itself.

610 For this reason, we believe that our example does not support the view that  
611 computational models are partial descriptions or that computational models are  
612 explanatory only because they describe causal relations. Instead, this reinforcement  
613 learning example is more consistent with the view that computational properties  
614 play an invaluable role in the explanation of cognitive phenomena.

615 Nonetheless, reinforcement learning is just one example of computational models of  
616 cognitive capacities. Future investigation of other computational models will be  
617 telling regarding the relation between computation and implementation.

## 618 **7 Conclusions**

619 After raising the problem of how computational explanations integrate in the  
620 mechanistic hierarchy, we analyzed reinforcement learning as an example of a

621 computational model in neuroscience and reviewed two possible pictures of the  
622 relations between computation and implementation in the mechanistic hierarchy.  
623 On the one-hierarchy picture computational and their implementational properties  
624 reside in the same level(s) of explanation. On the two-hierarchy picture  
625 computational and implementational properties reside in different computational  
626 and implementational hierarchies. We concluded that both pictures are possible  
627 regarding the reinforcement learning example, but that scientific practice does not  
628 align with the view that computational models are merely mechanistic sketches.

## 629 **Bibliography**

- 630 Bechtel, W. and Shagrir, O. (2015) 'The Non-Redundant Contributions of Marr's  
631 Three Levels of Analysis for Explaining Information-Processing Mechanisms', *Topics*  
632 *in Cognitive Science*, 7, pp. 312–322.
- 633 Behrens, T. E. J. *et al.* (2007) 'Learning the value of information in an uncertain  
634 world', *Nature Neuroscience*, 10, pp. 1214–1221. doi: 10.1038/nn1954.
- 635 Boone, W. and Piccinini, G. (2016) 'The cognitive neuroscience revolution', *Synthese*,  
636 193, pp. 1509–1534.
- 637 Botvinick, M. M. (2012) 'Hierarchical reinforcement learning and decision making',  
638 *Current Opinion in Neurobiology*, 22, pp. 956–962. doi: 10.1016/j.conb.2012.05.008.
- 639 Botvinick, M., Niv, Y. and Barto, A. (2009) 'Hierarchically organized behavior and its  
640 neural foundations: A reinforcement learning perspective', *Cognition*, 113, pp. 262–  
641 280. doi: 10.1016/j.cognition.2008.08.011.Hierarchically.
- 642 Chirimuuta, M. (2014) 'Minimal models and canonical neural computations: the  
643 distinctness of computational explanation in neuroscience', *Synthese*, 191, pp. 127–  
644 153.
- 645 Chirimuuta, M. (2018) 'Explanation in Computational Neuroscience: Causal and Non-  
646 causal', *The British Journal for the Philosophy of Science*, 69, pp. 849–880. doi:  
647 10.1093/bjps/axw034.
- 648 Coelho Mollo, D. (2018) 'Functional individuation, mechanistic implementation: the  
649 proper way of seeing the mechanistic view of concrete computation', *Synthese*, 195,  
650 pp. 3477–3497. doi: 10.1007/s11229-017-1380-5.
- 651 Craver, C. F. (2016) 'The Explanatory Power of Network Models', *Philosophy of*  
652 *Science*, 83, pp. 698–709.
- 653 Craver, C. F. and Povich, M. (2017) 'The directionality of distinctively mathematical  
654 explanations', *Studies in History and Philosophy of Science*, 63, pp. 31–38. doi:  
655 10.1016/j.shpsa.2017.04.005.

656 Cummins, R. (1983) *The Nature of Psychological Explanation*. MIT Press.

657 Cummins, R. (2000) “‘How does it work?’ vs. ‘What are the laws?’ Two conceptions  
658 of psychological explanation.’, in Keil, F. and Wilson, R. A. (eds) *Explanation and*  
659 *Cognition*. MIT Press, pp. 117–145.

660 Dewhurst, J. (2018) ‘Individuation without Representation’, *The British Journal for*  
661 *the Philosophy of Science*, 69, pp. 103–116. doi: 10.1093/bjps/axw018.

662 Doya, K. (2000) ‘Complementary roles of basal ganglia and cerebellum in learning  
663 and motor control’, *Current Opinion in Neurobiology*, 10, pp. 732–739. doi:  
664 10.1016/S0959-4388(00)00153-7.

665 Doya, K. (2008) ‘Modulators of decision making’, *Nature Neuroscience*, 11, pp. 410–  
666 416. doi: 10.1038/nn2077.

667 Egan, F. (2017) ‘Function-Theoretic Explanation and Neural Mechanisms’, in Kaplan,  
668 D. M. (ed.) *Explanation and Integration in Mind and Brain Science*. Oxford University  
669 Press, pp. 145–163.

670 Elber-Dorozko, L. and Loewenstein, Y. (2018) ‘Striatal action-value neurons  
671 reconsidered’, *eLife*, 7, p. e34248. doi: 10.7554/eLife.34248.

672 Fodor, J. (1968) *Psychological Explanation: An Introduction To The Philosophy Of*  
673 *Psychology*. Random House.

674 Fodor, J. (1980) ‘Methodological solipsism considered as a research strategy in  
675 cognitive psychology’, *Behavioral and Brain Sciences*, 3, pp. 63–73.

676 Fodor, J. (1994) *The elm and the expert*. MIT Press.

677 Fodor, J. A. (1975) *The Language of Thought*. Harvard University Press.

678 Haimovici, S. (2013) ‘A Problem for the Mechanistic Account of Computation’,  
679 *Journal of Cognitive Science*, 14, pp. 151–181.

680 Harbecke, J. (under review) ‘Multiple Level Hierarchies in Cognitive Neuroscience  
681 and the Mechanistic-Computational Model of Explanation’.

682 Haugeland, J. (1981) ‘Semantic Engines: an Introduction to Mind Design’, in  
683 Haugeland, J. (ed.) *Mind Design, philosophy, Psychology, Artificial Intelligence*. MIT  
684 Press.

685 Hollerman, J. R. and Schultz, W. (1998) ‘Dopamine neurons report an error in the  
686 temporal prediction of reward during learning’, *Nature neuroscience*, 1, pp. 304–9.  
687 doi: 10.1038/1124.

688 Hoshi, E. *et al.* (2005) ‘The cerebellum communicates with the basal ganglia’, *Nature*  
689 *Neuroscience*, 8, pp. 1491–1493. doi: 10.1038/nn1544.

690 Huneman, P. (2010) ‘Topological explanations and robustness in biological sciences’,  
691 *Synthese*, 177, pp. 213–245.

692 Ito, M. and Doya, K. (2009) 'Validation of Decision-Making Models and Analysis of  
693 Decision Variables in the rat basal ganglia', *The Journal of Neuroscience*, 29(31), pp.  
694 9861–9874. doi: 10.1523/JNEUROSCI.6157-08.2009.

695 Ito, M. and Doya, K. (2011) 'Multiple representations and algorithms for  
696 reinforcement learning in the cortico-basal ganglia circuit', *Current Opinion in*  
697 *Neurobiology*, 21, pp. 368–373. doi: 10.1016/j.conb.2011.04.001.

698 Kable, J. W. and Glimcher, P. W. (2009) 'The Neurobiology of Decision: Consensus  
699 and Controversy', *Neuron*. Elsevier Inc., 63(6), pp. 733–745. doi:  
700 10.1016/j.neuron.2009.09.003.

701 Kandel, E. R. *et al.* (2013) *Principles of Neural Science*. Fifth. New York: McGraw-Hill.

702 Kaplan, D. M. (2011) 'Explanation and description in computational neuroscience',  
703 *Synthese*, 183, pp. 339–373.

704 Kaplan, D. M. (2017) 'Neural computation, multiple realizability, and the prospects  
705 for mechanistic explanation', in Kaplan, D. M. (ed.) *Explanation and Integration in*  
706 *Mind and Brain Science*. Oxford University Press, pp. 164–189.

707 Kaplan, D. M. and Craver, C. F. (2011) 'The Explanatory Force of Dynamical and  
708 Mathematical Models in Neuroscience : A Mechanistic Perspective', *Philosophy of*  
709 *Science*, 78, pp. 601–627.

710 Lange, M. (2013) 'What Makes a Scientific Explanation Distinctively Mathematical?',  
711 *The British Journal for the Philosophy of Science*, 64, pp. 485–511. doi:  
712 10.1093/bjps/axs012.

713 Lee, E. *et al.* (2015) 'Injection of a Dopamine Type 2 Receptor Antagonist into the  
714 Dorsal Striatum Disrupts Choices Driven by Previous Outcomes , But Not Perceptual  
715 Inference', *The Journal of Neuroscience*, 35, pp. 6298–6306. doi:  
716 10.1523/JNEUROSCI.4561-14.2015.

717 Li, J. and Daw, N. D. (2011) 'Signals in Human Striatum Are Appropriate for Policy  
718 Update Rather than Value Prediction', *Journal of Neuroscience*, 31, pp. 5504–5511.  
719 doi: 10.1523/JNEUROSCI.6316-10.2011.

720 Marr, D. (1982) *Vision: A Computational Investigation into the Human*  
721 *Representation and Processing of Visual Information*. MIT Press.

722 Milkowski, M. (2013) *Explaining the Computational Mind*. MIT Press.

723 Mnih, V. *et al.* (2016) 'Human-level control through deep reinforcement learning',  
724 *Nature*, 518, pp. 529–533. doi: 10.1038/nature14236.

725 Mongillo, G., Shteingart, H. and Loewenstein, Y. (2014) 'The misbehavior of  
726 reinforcement learning', *Proceedings of the IEEE*, 102, pp. 528–541. doi:  
727 10.1109/JPROC.2014.2307022.

728 O'Doherty, J. P. *et al.* (2004) 'Dissociable Role of Ventral and Dorsal Striatum in  
729 Instrumental Conditioning', *Science*, 304, pp. 452–454. doi:

- 730 10.1126/science.1094285.
- 731 Piccinini, G. (2015) *Physical Computation: A Mechanistic Account*. Oxford University  
732 Press.
- 733 Piccinini, G. and Bahar, S. (2013) 'Neural Computation and the Computational Theory  
734 of Cognition', *Cognitive Science*, 34, pp. 453–488.
- 735 Piccinini, G. and Craver, C. F. (2011) 'Integrating psychology and neuroscience:  
736 functional analyses as mechanism sketches', *Synthese*, 183, pp. 283–311.
- 737 Rathkopf, C. (2015) 'Network representation and complex systems', *Synthese*, 195,  
738 pp. 55–78.
- 739 Rusanen, A. and Lappi, O. (2016) 'On computational explanations', *Synthese*, 193, pp.  
740 3931–3949.
- 741 Samejima, K. *et al.* (2005) 'Representation of Action-Specific Reward Values in the  
742 Striatum', *Science*, 310, pp. 1337–1340. doi: 10.1126/science.1115270.
- 743 Schultz, W., Dayan, P. and Montague, P. R. (1997) 'A Neural Substrate of Prediction  
744 and Reward', *Science*, 275, pp. 1593–1599. doi: 10.1126/science.275.5306.1593.
- 745 Shagrir, O. (2006) 'Why we view the brain as a computer', *Synthese*, 153, pp. 393–  
746 416.
- 747 Shagrir, O. (2016) 'Advertisement for the Philosophy of the Computational Sciences',  
748 in Paul Humphreys (ed.) *The Oxford Handbook of Philosophy of Science*. Oxford  
749 University Press, pp. 15–42.
- 750 Shagrir, O. and Bechtel, W. (2017) 'Marr's Computational Level and Delineating  
751 Phenomena', in Kaplan, D. M. (ed.) *Explanation and Integration in Mind and Brain  
752 Science*. Oxford University Press, pp. 190–214.
- 753 Shapiro, L. A. (2017) 'Mechanism or Bust? Explanation in Psychology', *The British  
754 Journal for the Philosophy of Science*, 68, pp. 1037–1059.
- 755 Shteingart, H. and Loewenstein, Y. (2014) 'Reinforcement learning and human  
756 behavior', *Current Opinion in Neurobiology*, 25, pp. 93–98. doi:  
757 10.1016/j.conb.2013.12.004.
- 758 Shteingart, H., Neiman, T. and Loewenstein, Y. (2013) 'The role of first impression in  
759 operant learning', *Journal of Experimental Psychology: General*, 142, pp. 476–488.  
760 doi: 10.1037/a0029550.
- 761 Sprevak, M. (2010) 'Computation, individuation, and the received view on  
762 representation', *Studies in History and Philosophy of Science Part A*, 41, pp. 260–270.
- 763 Stich, S. (1983) *From Folk Psychology to Cognitive Science: The Case Against Belief*.  
764 MIT Press.
- 765 Sutton, R. S. and Barto, A. G. (1998) *Reinforcement Learning: An Introduction*. MIT



766 Press.

767 Tai, L.-H. *et al.* (2012) 'Transient stimulation of distinct subpopulations of striatal  
768 neurons mimics changes in action value', *Nature neuroscience*, 15, pp. 1281–9. doi:  
769 10.1038/nn.3188.

770 Wang, A. Y., Miura, K. and Uchida, N. (2013) 'The dorsomedial striatum encodes net  
771 expected return, critical for energizing performance vigor.', *Nature neuroscience*, 16,  
772 pp. 639–47. doi: 10.1038/nn.3377.

773 Watkins, C. J. C. H. and Dayan, P. (1992) 'Q-Learning', *Machine Learning*, 8, pp. 279–  
774 292.

775 Weiskopf, D. A. (2011) 'Models and mechanisms in psychological explanation',  
776 *Synthese*, 183, pp. 313–338.

777