

## **Control without controllers: Towards a distributed neuroscience of executive control**

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## Abstract

Executive control refers to the regulation of cognition and behavior by mental processes and is a hallmark of higher cognition. Most approaches to understanding its mechanisms begin with the assumption that our brains have anatomically segregated and functionally specialized control modules. The modular approach is intuitive: control is conceptually distinct from basic mental processing, so an organization that reifies that distinction makes sense. An alternative approach sees executive control as self-organizing principles of a distributed organization. In distributed systems, control and controlled processes are co-localized within large numbers of dispersed computational agents. Control then is often an emergent consequence of simple rules governing the interaction between agents. Because these systems are unfamiliar and unintuitive, here we review several well-understood examples of distributed control systems, group living insects and social animals, and emphasize their parallels with neural systems. We then re-examine the cognitive neuroscience literature on executive control for evidence that its neural control systems may be distributed.

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## Main Text

### I. Introduction

Executive control refers to the brain's ability to regulate its own processing. It coordinates multiple competing demands, controls attention, gates working memory, and encodes and retrieves long-term memories. It also maintains and switches task set, inhibits disadvantageous actions, and regulates the explore/exploit tradeoff and curiosity (Miller & Cohen, 2001; Shiffrin & Schneider, 1977; Braver & Barch, 2006; Cole & Schneider, 2007; Miller, 2000a; Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004; Kidd & Hayden, 2015). Understanding executive control is critical for understanding self-control and its failures (Aron, Robbins, & Poldrack, 2014; Knoch & Fehr, 2007; Hare & Rangel, 2009). More broadly, failures of executive control are hallmarks of many diseases, including addiction, depression, and obsessive-compulsive disorder, and successful treatments of these diseases often target executive control (e.g. Milad & Rauch, 2012; Ursu et al., 2003; Volkow & Fowler, 2000; Kalivas & Volkow, 2005).

A brain can be understood as a *control system*, a collection of interacting components within an organizational structure that produces adaptive actions based on information about the current state of the internal and external worlds (Pezzulo & Cisek, 2016; Gallistel, 2013; Lashley, 1951). As we process sensory inputs and generate actions, the brain monitors that processing and, if it detects the need to change, it regulates it. But how is executive control in the brain implemented by the interactions of its constituent parts, individual neurons?

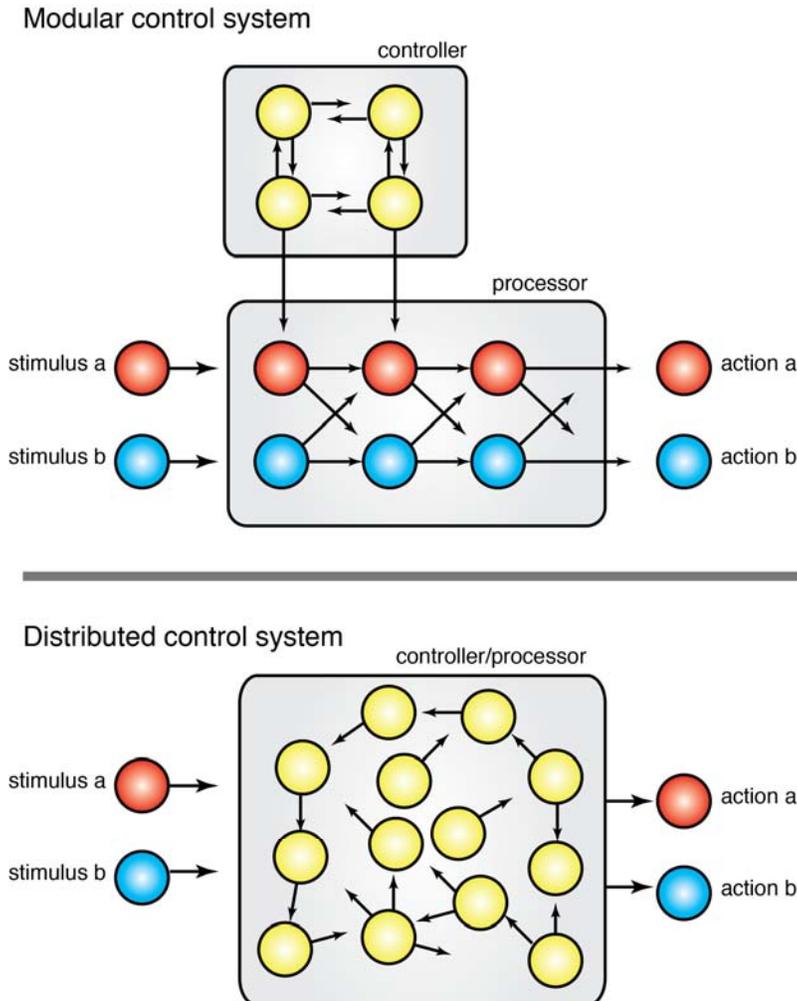
#### Modular and distributed control systems

The standard approach to understanding control starts with the assumption of modularity. In a modular control system, regulation is derived from a central controller, which is a discrete subsystem with a specialized function. In a modular system, it is theoretically possible to draw a line through anatomical space separating localized control regions or circuits (often the prefrontal cortex and striatum) from more basic processing (caudal cortical) regions (Botvinick et al, 2001; Miller & Cohen 2001; Miller, 2000). This specialization means that control regions (or networks) regulate, but do not participate in, the underlying stimulus-to-action transformation processes (Figure 1). Such a view is consistent with a long tradition emphasizing the brain's modular architecture (Fodor, 1983; Minsky, 1988; Kanwisher, Mcdermott, & Chun 1997; Bertolero, Yeo, & Desposito 2015). But it is not the only possible view.

The alternative approach envisions executive control as distributed processes in which there is no dedicated and specialized controller (Figure 1). Instead, in a distributed control system, regulatory functions are dispersed across a large number of individual elements or carried out by the interaction among them (Couzin, 2009; Sumpter, 2006). In most such systems control elements are co-localized with processing elements, and those elements have somewhat autonomous function. For this reason they are often called *agents*. These agents (or any other individual elements in a distributed control system) sense the properties of their local environment and adjust their own behavior based on

65 simple rules. Agents normally have no knowledge of the overall state of the system, and  
66 the response of the system as a whole is often qualitatively dissimilar from those of the  
67 elements. In other words, in such systems, control is often an *emergent* function  
68 (McClelland et al., 2010; Hofstadter, 1985, Ch. 25; Mitchell, 2009).

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**Figure 1.** Contrasting organizations of modular and distributed control systems. Within modular control systems, processing and control elements are distinct and localized to specific areas. By contrast distributed systems combine control and processing elements, often into individual agents.

77 The distributed viewpoint derives inspiration from early studies on cybernetic,  
78 connectionist, and parallel distributed processing models (Rummelhart et al., 1988;  
79 Weiner et al., 1944; Grossberg, 1974; Hopfield, 1982). As noted in a review of the topic  
80 by Botvinick and Cohen (2014), the connectionist heyday of the late 70's and early 80's  
81 coincided with the development of formal ideas of control (Posner & Snyder, 1975;  
82 Shiffrin & Schneider, 1977; Norman & Shallice, 1986; Baddeley & Hitch, 1974). It is  
83 ironic then that almost all models of executive control, even relevant PDP models, take as  
84 given that control is functionally and anatomically modular (Botvinick & Cohen, 2014).  
85 Nonetheless, history has vindicated this approach: the modular idea is well supported by

86 empirical data. Specifically, neuroscientific research consistently points to dorsal  
87 prefrontal structures (especially the dorsal anterior cingulate cortex, dACC, see below),  
88 as well as superior parietal cortex and parts of the brainstem as the brain's control system  
89 (Holroyd & Coles, 2002; Botvinick & Cohen, 2014; Ridderinkoff et al., 2004; Shenhav,  
90 Botvinick & Cohen, 2013; Miller & Cohen, 2001; Sleezer & Hayden, 2016; Floresco,  
91 2015; Mansouri et al., 2007).

### 92 93 **Revisiting the distributed processing view**

94 Still, we believe that it is time to revisit a distributed approach to control. Several  
95 factors motivate this belief. First, our understanding of the neuronal (i.e. single unit)  
96 responses of the putative executive regions is only now maturing. Some of this work  
97 emphasizes the broad overlap in functions of the prefrontal and posterior regions; these  
98 functions appear to include both processing and executive roles (Cisek & Kalaska 2010;  
99 Kim & Shadlen, 1999; Chafee & Goldman-Rakic, 1998; Postle, 2006; Awh & Jonides,  
100 2001; Sleezer & Hayden, 2016a; Sleezer, Castagno, & Hayden, 2016). Second, new  
101 anatomical and functional techniques emphasize the fundamentally non-modular  
102 organization of the brain (Misic & Sporns, 2016; Wang et al., 2015; Farah, 1994; Kristan  
103 & Shaw, 1997; Plaut, 1995). Third, major recent advances in computation have come  
104 from abandoning classic (GOFAD)-style symbol manipulating systems in favor of deep  
105 learning algorithms that are distributed and recurrent (e.g. Lecun, Bengio, & Hinton,  
106 2015; Hinton & Salakhutdinov, 2006). These approaches highlight the power and  
107 flexibility of non-modular network organizations. Finally, recent years have seen a  
108 greater understanding of the mechanisms of distributed control in non-brain biological  
109 systems, leading to a greater appreciation of the strengths and of the biological  
110 plausibility of such systems (Couzin, 2009; Passino, Seeley, & Vischer, 2007).

111 Reified models of executive control – in which conceptual elements like monitor,  
112 controller, and processor have direct correspondence with neuroanatomy – are intuitive.  
113 But distributed models are less so. To mitigate this problem here we offer a summary of  
114 the basic principles of distributed control systems, with an emphasis on natural examples.

## 115 116 **II. Principles of distributed control systems**

### 117 118 **Principle 1: Horizontal information flow**

119 Within a modular control system, information flows linearly from lower level  
120 processing units to the controller. By contrast information flow within distributed systems  
121 is characterized by horizontal communication between adjacent members. In other words,  
122 information is derived from neighbors, not from a central communicator. Consequently,  
123 no single member of a distributed system is knowledgeable about the entire system. Each  
124 member can know what their neighbor is doing, and possibly what their neighbor knows,  
125 through localized interactions.

126 A good example of information flow within a distributed system is a herd of  
127 baboons on the move (*Papio anubis*, Couzin & Krause, 2003; Strandberg et al, 2015).  
128 Even though they have a hierarchical dominance system, no single member of the troop  
129 knows for sure where to go but several members have some limited and likely noisy  
130 knowledge (Figure 2). The wisdom of the crowd is better than any individual's guess, as  
131 in many collectively moving animals – including humans (Codling, Pitchford, &

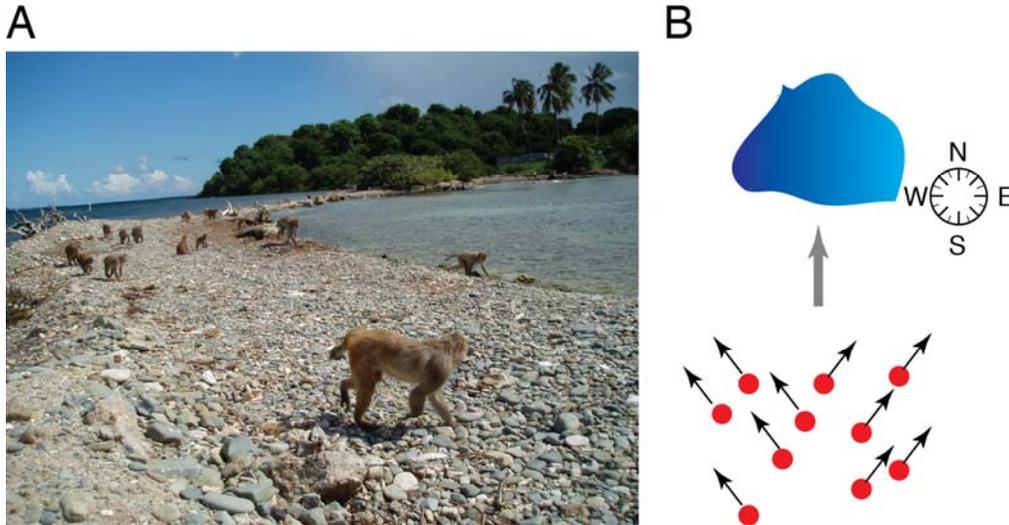
132 Simpson, 2007; Simons, 2004; Hamilton, 1967; Bergman & Donner, 1964; Walraff,  
133 1978; Mallon, Pratt, & Franks, 2001; Conradt & Roper 2003). The baboon troop thus  
134 uses a collective decision-making strategy. Individuals begin to head off towards their  
135 best guess and as they do this, troop members compute the average of the members they  
136 observe. Unlike in a modular system each member may be simultaneously a decision  
137 maker and a data point for other decision makers.

138 Normally this strategy leads efficiently to a rapid consensus (Couzin & Krause,  
139 2003; Conradt & Roper, 2003). In cases where there are two different modal preferences  
140 – say, when northeast and northwest are both good directions but true north is not, this  
141 averaging strategy leads to a suboptimal choice (Figure 2B). For this reason individuals  
142 should be – and are - sensitive to bimodal distributions among the group and, in that case,  
143 randomly choose one of the two modal directions (Strandberg et al, 2015). Similar  
144 patterns are observed in pigeons and human crowds (Biro et al., 2006; Dyer et al, 2008).

145 In this example, the input is the environmental clues (including memories) about the  
146 best direction to head and the output is a group path. Information is distributed across  
147 individual troop members who communicate locally with each other. Drawing from the  
148 local interactions among members, the group chooses a better output than all the  
149 constituent individuals. The decision is also controlled in a closed-loop manner: the  
150 group can monitor its own performance (it can detect split voting) and regulate its voting  
151 strategy (averaging to bifurcation-then-averaging), even though no individual serves as  
152 the specialized monitor or regulator. Instead, monitoring and control proceed through  
153 local, horizontal connections between members.

154 The idea of horizontal flow of information from adjacent members is also often a  
155 description of neuroanatomical organization. Neurons, like troop members, tend to have  
156 limited view of the activity of the whole, limited ability to communicate with the whole,  
157 incomplete information, no knowledge of the larger factors that determine the group's  
158 well-being, and no obvious leadership. However, neurons do have a rich network of  
159 connections to adjacent neighbors and cortical areas that supports a localized flow of  
160 information. While the brain also has centralized global signaling, in the form of  
161 neuromodulators (and possibly cortical oscillations), the bandwidth of these signals is  
162 limited and the timing may be too slow to affect on-line decision processes. Similar to a  
163 baboon troop, the information gained from equal and adjacent members has a large effect  
164 on the regulation of its neural function.

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167 **Figure 2.** Group movement strategies often illustrate the principle of horizontal  
168 information transfer. **A.** Rhesus monkey troops on Cayo Santiago migrate multiple times  
169 each day and may use distributed consensus procedures to choose a direction. **B.**  
170 Cartoon birds eye view illustrating split voting situation. If the troop is split between a  
171 northeast and a northwest direction, the consensus will not be the average (north) but  
172 one of the two modal directions.  
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### 174 **Principle 2: Stigmergy**

175 In the case of the baboons, it is notable that the control signal is the movement of  
176 neighbors. Thus, in a strongly non-modular way, the control signal is precisely the output  
177 of the underlying process (also movement of individuals). It is a *stigmergic* system  
178 (Bonabeau, Dorigo, & Theraulaz, 1999; Theraulaz, Bonabeau, & Deneubourg, 1998;  
179 Couzin, 2009).

180 A familiar example of stigmergic signaling is lawn shortcut generation on college  
181 campuses. A student following the trod path also – weakly but surely – strengthens it  
182 (Figure 3.). Another example is pheromonal trails in foraging ants (Hölldobler &  
183 Wilson, 1990; Wilson, 1971). As a scout forages she lays a scent that other scouts will  
184 follow to valuable food sources. The scent evaporates quickly, so rich food patches,  
185 which attract many ants, will have stronger paths leading to them. An ant that, by chance,  
186 discovers a shortcut will produce a trail with a stronger scent (because, being shorter, it  
187 takes less time to traverse and thus has more scent, Beckers & Deneubourg, 1992). In this  
188 way, pheromones allow ant colonies to find rich food sources and develop shortest path  
189 routes without any centralized control (Aron, Beckers, & Deneubourg, 1993; Jackson &  
190 Chaline, 2007; Beekman, Sumpter, & Ratnieks, 2001).  
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193 **Figure 3.** Humans can collectively identify, create, and maintain efficient paths  
194 across lawns on college campuses. Reproduced with permission from “Modeling the  
195 evolution of human trail systems” (Helbing, Keltsch, & Molnar, 1997).  
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197 Another example of stigmergic control comes from the process of neural  
198 differentiation of sensory organ precursors within the developing fly brain (*Drosophila*  
199 *melanogaster*) (Navalakha & Bar-Joseph, 2011). During development some cells within  
200 the neural clusters of the fly brain become sensory organ precursors (SOPs); these cells  
201 form the backbone of the sensory system later in development. Determination of which  
202 cells become SOPs follows an algorithmic process that produces a maximally  
203 independent set distributed throughout the brain. Functionally each cell will propose itself  
204 as a possible SOP. If any neighboring cell has already become a SOP the proposing cell  
205 will not differentiate. As a consequence of this process the likelihood of an unconnected  
206 cell differentiating increases with time (Afek et al., 2011; Navalakha & Bar-Joseph,  
207 2011). By using information about the structure of neighboring cells, each cell is able to  
208 differentiate appropriately so that the whole brain achieves an equal spacing of sensory  
209 organ precursors. The brain cells do this rapidly and without the need for a monitor or  
210 knowledgeable controller sending distinct control signals. All the monitoring and control  
211 that is needed occurs locally, within each cell.

212 Principles of stigmergy within executive control processes relates to neural function  
213 quite directly. Neurons produce chemical outputs that modulate responses of downstream  
214 neurons. These outputs are both the computational outputs of the neurons and a way to  
215 modulate activity of their neighbors. In the short term, excitatory and inhibitory outputs  
216 increase and reduce, respectively, the likelihood that the target will fire. In the long term,  
217 activity (especially coincident activity) promotes synaptic plasticity thus up- or down-  
218 regulating that target’s firing on longer timescales. Within cortical regions, these  
219 localized interactions could very well lead to emergent control signals without the need  
220 for a dedicated controller (Couzin, 2009).  
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### 222 **Principle 3: Feedback loops**

223 Feedback is a powerful tool in any dynamical system. It can have positive effects.  
224 When fish school, a few peripheral individuals may detect a potential predator and turn  
225 away from it (Treherne & Foster, 1981; Couzin & Krause, 2003). Neighbors who follow  
226 an average-direction rule then turn and also affect their neighbors, the effect multiplies,  
227 and the traveling wave of turning fish turns the whole school away. The amplification  
228 protects many more fish than were able to detect the predator. Similarly, feedback loops  
229 are a mainstay of other distributed leaderless systems; even audience clapping, for  
230 example, can depend on feedback effects (Néda et al., 2000)

231 However, feedback loops can be dangerous as well (Giraldeau & Valone, 2002).  
232 Simple effects can snowball and, because the system is distributed, there is no central  
233 controller to stop it. For example, ants leaving a pheromonal trace can find their own  
234 trail, and start going in a circle – a literal feedback loop called an ant mill (Delsuc, 2003).  
235 Another important example of a feedback loop is a marketplace bubble (Porter & Smith,  
236 1994; Smith, Suchanek, & Williams, 1988). If a speculator believes a commodity will go  
237 up in price, she may bid a slightly greater price than the current one. This bidding will  
238 serve as a signal to other investors that the commodity may be a wise investment. As they  
239 bid up the price, their initial assessment will be proven to be right, and other investors  
240 will gain interest. This pattern can lead to runaway prices, but only up to a point; as soon  
241 as this point is reached, the price will crash.

242 The tendency to boom and bust can lead to market instability and to  
243 underinvestment. In marketplaces, centralized control (such as trading limits) can solve  
244 these problems. Without that kind of control, avoiding these kinds of malign feedback  
245 loops requires careful calibration of the rules each individual follows. Such calibrations  
246 often involve complementary negative feedback loops (Grünbaum, 1998). The analogy to  
247 brains, which have many overlapping positive and negative feedback loops, is quite  
248 direct.

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#### 250 **Principle 4: Self-organization through simple rules**

251 Many distributed control systems are self-organized (Sumpter, 2006). Classic  
252 examples of self-organization include bird flocks and fish schools (Aoki, 1982; Couzin,  
253 2009; Reynolds, 1987). No leader bird rallies its mates and tells them where to fly; nor  
254 does a leader monitor the flock and guide its performance like coxswain on a crew team.  
255 Instead, the structure of the bird flock is a consequence of several simple principles  
256 followed by all individuals. These include rules about distance between adjacent birds  
257 (not too far and not too close, more or less) and rules about when to turn (follow the  
258 group average, Couzin & Krause, 2003). The specific rules, not a leader-bird, determine  
259 the shape of the flock (Figure 4).



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**Figure 4.** Simple rules of distance and spacing determine the shapes of both fish schools and bird flocks. [Fish picture: Gordon Firestein - Seacology USA, Bird Flock: Faisal Akram]

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Self-organization is an appealing principle because it is easy to implement and is robust to degradation (Sumpter, 2006). In contrast, the centralized systems are vulnerable to the loss of the controller: Remove a switch and the whole railyard breaks down; remove the coxswain and the rowers start hitting each other's oars; remove one bird and the flock swiftly adjusts. Self-organization also allows complex adaptive behavior without programming expensive control systems. Self-organized systems can be "fast, cheap, and out of control" (Brooks & Flynn, 1989). These features – ease of implementation, graceful degradation, and robustness, makes it appealing for analyzing neural systems. One well-known example of a self-organizing system in neurons is central pattern generators, in which the activity of the ensemble is an emergent product of the interactions of the elements, none of which follows the pattern in miniature.

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This does not mean all distributed systems are leaderless. There are many contexts in which formation of leadership is favored (Couzin et al., 2005; Fischhoff et al., 2007; Dyer, 2009; Robson & Traniello, 1999; Reeb, 2000). Dominance hierarchies and other leadership structures are selected in many species, although leadership is seldom absolute. And there are intermediate cases - even in the case of baboons, some individuals are recognized as having greater knowledge of the right path and their opinion is more highly weighted (Strandburg et al., 2015).

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Presumably, we can classify control systems on a spectrum from fully distributed and leaderless to strictly segregated and hierarchical; the specific organization observed for any system will depend on the environment in which it evolved. This fact is important to remember when considering neural systems, which may have some specialization of function (Botvinick et al., 2001; Rougier et al., 2005; Kanwisher, McDermott, & Chun, 1997).

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### **Principle 5: Quorum-sensing**

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Agents in distributed systems have very limited field of view in their monitoring capabilities. In other words, it is often difficult to see the forest for the trees. But sometimes it is critical to see the forest to make the best decision. In these cases, agents must engage in *quorum-sensing*: a type of consensus-based control mechanism wherein a set threshold or quorum determines the course of action (Mitchell, 2009).

296           There are many mechanisms for quorum-sensing; what unites them is that they do  
297 not require centralized control. For example, bacteria can produce diffusible chemicals  
298 (which can serve as a type information) and chemical concentration in the environment  
299 gives a measure of quorum (Waters and Bassler, 2005). One critical feature of any  
300 consensus-seeking measure is that it must terminate; it should also do so relatively  
301 quickly. Failures to do so can be costly, as in the case of Buridan's ass (Lindauer, 1957;  
302 Pais et al., 2013).

303           Often, individuals can sense the state of conspecifics in their local environment and  
304 extrapolate to an estimate of group state. Simply averaging the states of neighbors can be  
305 helpful in some circumstances, as in bird flocks and some fish schools. One study showed  
306 that an individual schooling three-spine stickleback fish (*Gasterosteus aculeatus*) can  
307 adopt a non-linear monitoring function that produces better group behavior emergently  
308 (Ward et al., 2008). Specifically, groups of fish tended to ignore information from single  
309 neighbor but responded when two fish conveyed the same information. This non-linear  
310 criterion can reduce the probability of amplifying noise but can still effectively detect  
311 signals.

312           The need for agents to sense the properties of the whole, or of large subgroups, is a  
313 major problem in brain systems as a whole. This problem is acute in executive control  
314 systems, which often rely on changing processing as a function of global conditions.  
315 Without holistic integrating neurons, it is difficult to imagine a direct solution to the  
316 problem. For this reason, studies of quorum-sensing systems, which solve the problem  
317 indirectly, are particularly likely to be helpful in understanding the neural basis of  
318 control.

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### 320           **III. Distributed solutions to classic executive control problems**

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322           Studies of executive control tend to focus on processes for solving a familiar set of  
323 cognitive problems. Prominent among these processes are regulation of stop/go behavior,  
324 speed/accuracy tradeoffs and conflict detection and resolution (Bogacz et al., 2009; Aron,  
325 Robbins, & Poldrack, 2014; Botvinick et al., 1999; Miller & Cohen, 2001). These  
326 operations have analogues outside of neuroscience, including in distributed control  
327 systems of natural and artificial mechanisms. In this section, we investigate how some  
328 examples of distributed control systems handle these executive control problems through  
329 the fundamental elements outlined above. Other important executive functions, which we  
330 do not consider, include working memory, attention, task set maintenance and switching,  
331 regulating the balance of explore vs. exploit behavior, and aspects of reinforcement  
332 learning. Several of these have likely correlates in distributed control systems as well.  
333 See, for example, (Couzin et al., 2002; Couzin, 2009; and Passino, Seeley, & Visscher,  
334 2007) for speculation about how distributed processing systems can implement working  
335 memory, attention, and regulation of long-term memories.

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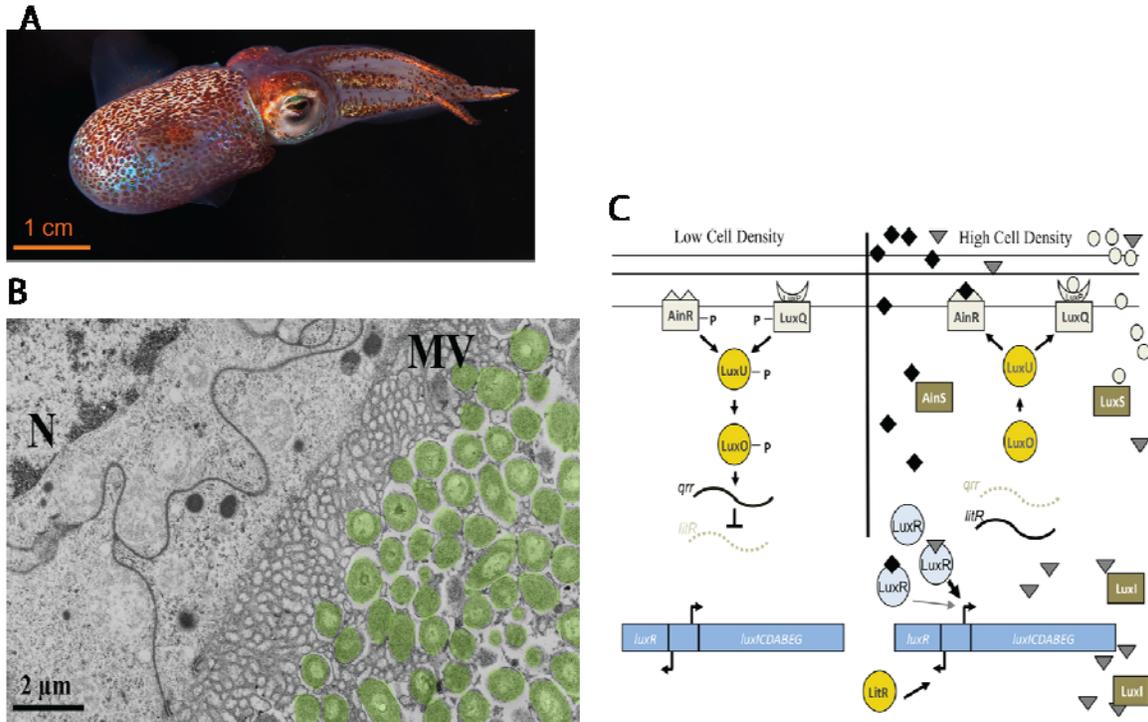
#### 337           **Stopping and going: *Vibrio fischeri* bacteria**

338           Initiation and inhibition of behavior is a simple and important executive function  
339 (Jin & Costa, 2010; Schall, 2001; Aron, Robbins, & Poldrack, 2004; Niv et al., 2007;  
340 Hampshire & Sharp, 2015; Kacelnik et al., 2011). Coordination of these two antagonistic  
341 processes can produce both simple responses and complex behaviors. Stop/go behavior

342 involves elements like precise timing, inhibition of prepotent responses, and control of  
343 vigor. Another important but less well-appreciated requirement is avoiding intermediate  
344 responses, so that the system can either fully stop or fully go, without drifting between  
345 the two extremes. In other words, being indeterminate can be costly and even lethal in  
346 urgent situations so that the distributed system has to be able to deal with this problem.

347 Our example of stop/go control in a distributed control system comes from the  
348 luminous bacterium *Vibrio fischeri* (Waters & Bassler, 2005; Nealson & Hastings, 1979;  
349 Miller & Bassler, 2001). This single-celled organism lives in the light organ of the  
350 Hawaiian bobtail squid (*Euprymna scolopes*) and emits light when the squid hunts at  
351 night. The light serves to camouflage the squid that otherwise would be visible in the  
352 form of a moonlit silhouette to prey below it (Visick et al., 2000). During the day the  
353 squid hides from potential predators in the dirt and turns its eyes off by extruding most of  
354 the bacteria into the surrounding ocean. As the day progresses the remaining bacteria  
355 reproduce rapidly, and, by nightfall, have replenished their stock so that there are enough  
356 bacteria to serve as an effective camouflage.

357 The control problem comes from the fact that the bacteria must not luminesce  
358 during the day as they are reproducing. Instead they need to switch to lighting at night all  
359 at once. In other words, bioluminescence needs to be both inducible and repressible  
360 (Nealson & Hastings, 1979). Because of their reproduction pattern, they can do this by  
361 waiting until there is a quorum of other *V. fischeri* bacteria in the squid light organ. But  
362 how do they know how many others there are? Quorum sensing. *V. fischeri* release a  
363 chemical known as acyl-homoserine lactone (AHL). They then measure the concentration  
364 of this chemical in their local environment by the transcription activator protein LuxR,  
365 which creates a complex that induces transcription of genes needed for luminescence  
366 (Kaplan & Greenberg, 1985; Stevens & Dolan, 1994). The transcription process is only  
367 triggered when the local density of AHL reaches a predetermined threshold, which serves  
368 as a go signal for the bacteria (Figure 5).  
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**Figure 5. A.** Hawaiian squid (*Euprymna scolopes*). **B.** Image of *V. fischeri* embedding into microvilli of host epithelial cells. **C.** Illustration of control circuit for regulation of luminescence through chemical detection in *V. fischeri*. Credits: (A,B) reproduced with permission from “Divining the essence of symbiosis: Insights from the squid-vibrio model.” (McFall-Ngai, 2014). (C) reproduced with permission from “Gimme shelter: how vibrio fischeri successfully navigates an animals multiple environments” (Norsworthy & Visick, 2013).

There are several features used by the system to stop, i.e. to prevent premature luminescence. These features work by implementing negative feedback (Waters & Bassler, 2005). One feature is regulation of the stability of the constituent proteins: they are more stable when AHL is more concentrated (Zhu & Winans, 1999). Another is active pumping of AHL out of the cell: this process reduces cytoplasmic levels of AHL and thus dampens sensitivity until AHL concentration is high enough to overwhelm the pumping mechanism (Pearson et al., 1999).

Several features of this stop/go process are notable here for the curious neuroscientist. First, the system implements a clock-like function by taking advantage of the consistency in reproduction rates of its own members. No member or subgroup serves as a clock or other timer function. In other words, the timing function is an emergent property of the system. Second, there is no centralized site that tells the bacteria when to glow; each individual agent makes up its own tiny mind, but, because they are in the same environment, their activity is effectively coordinated through the localized cross-signaling of individual cells. Third, the system implements a specific and precise threshold-crossing process (a simple rule based on concentration levels of AHL), even though no abstract decision variable is calculated or represented. Finally, there is no need for any kind of modular self-control or inhibition. The lack of glowing (repressability) is

397 simply a consequence of the fact that there are insufficient concentrations of chemicals to  
398 drive the glowing; inhibition in this system is an emergent process (cf. Hampshire &  
399 Sharp, 2015).

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#### 401 **Speed-accuracy tradeoffs: ants**

402 A decision made without taking the time to gather all the evidence may not be as  
403 accurate as a deliberate one, but it will have the virtue of speed (Houston, Kacelnik, &  
404 McNamara, 1982). If time is costly (as when faced by an attacking predator) it may be  
405 worth going for the first good response, but if the decision-maker has all the time in the  
406 world, it's probably worth doing some pondering. Speed-accuracy tradeoffs are a staple  
407 of cognitive psychology (Busemeyer & Townsend, 1993; Wickelgren, 1977; Roitman &  
408 Shadlen, 2002; Chittka et al., 2003; Gigerenzer & Goldstein, 1996; Bogacz et al., 2010)  
409 and animal psychology (Chittka, Skorupski, & Raine, 2009). Like humans and animals,  
410 many distributed decision-making systems make speed-accuracy tradeoffs, including  
411 slime molds (*Physarum polycephalum*) and honeybees (*Apis mellifera*, Dussutour, Latty,  
412 & Beekman, 2010; Passino, Seeley, & Visscher 2007).

413 When looking for a new nest, individual ants (*Leptothorax albipennis*) leave the  
414 nest and evaluate potential locations within a few square meters (Franks et al., 2002;  
415 Franks et al., 2003). These ants prefer to live in small colonies in thin cracks in rocks and  
416 are therefore easy to study in laboratory conditions (Franks et al., 2002). An ant that finds  
417 a potential nest site will recruit other ants to evaluate it by leading a tandem run back to  
418 the site. Thus, each site is evaluated by a large number of individuals, each of whom  
419 presumably makes a worse (less accurate) decision than the cumulative choice of several  
420 ants. Unlike bees (see below) individual ants appear to evaluate and compare multiple  
421 sites, giving them more individual knowledge and requiring smaller quorum sizes (Franks  
422 et al., 2002; Pratt et al., 2002; Franks et al., 2003). If enough ants appear at a single site,  
423 scouts recognize a quorum, and the quorum catalyzes a change in their behavior; scouts  
424 now carry their nestmates to the new site and deposit them there (Pratt et al., 2002;  
425 Franks et al., 2002).

426 This whole search and quorum-sense process is slow but accurate. But if the  
427 situation calls for a fast decision (such as during windy weather or threat of predation),  
428 the ant colony can make a speed-accuracy tradeoff (Franks et al., 2003). Specifically,  
429 each ant can reduce the threshold it uses to decide whether to switch from tandem run  
430 recruitment mode to carrying mode. The tandem run, being slower, allows other ants  
431 more time to discover other sites; the carry terminates the process more quickly. The ant  
432 itself doesn't know explicitly about the speed-accuracy tradeoff; it just has an internal  
433 sense of weather and adjusts its quorum-sensing procedure – and the group's speed-  
434 accuracy tradeoff is an emergent consequence (Franks et al., 2003).

435 The neuroscience of the speed-accuracy tradeoff is not fully understood, but the  
436 parallels are easy to discern. It is believed that there is a threshold integration process for  
437 perceptual decisions (Bogacz et al., 2010). Recent work suggests it may involve changes  
438 in the baseline activity of neurons that serve as cortical integrators that bring them closer  
439 to threshold (Ivanoff, Branning, & Marois, 2008; VanVeen, Krug, & Carter, 2008),  
440 perhaps through disinhibition (Forstmann et al., 2008). Complementary research suggests  
441 that slower decisions involve inhibition from the subthalamic nucleus (Frank, Scheres, &  
442 Sherman, 2007; Aron & Poldrack, 2006). In either case, neurons encode a decision

443 variable that, in a distributed manner, represents the evidence in favor of the decision.  
444 While these models are not strictly distributed control models (because the thresholding  
445 is assumed to be separate from the accumulation), they have characteristics of it. A major  
446 goal of the stopping literature is to identify the key brain site that regulates stopping. The  
447 distributed control approach cautions that such a site may need not exist; instead of a site,  
448 there might be a neural mechanism at work, one that is not distinct from the sites of  
449 neurons that form the perception-action stream.

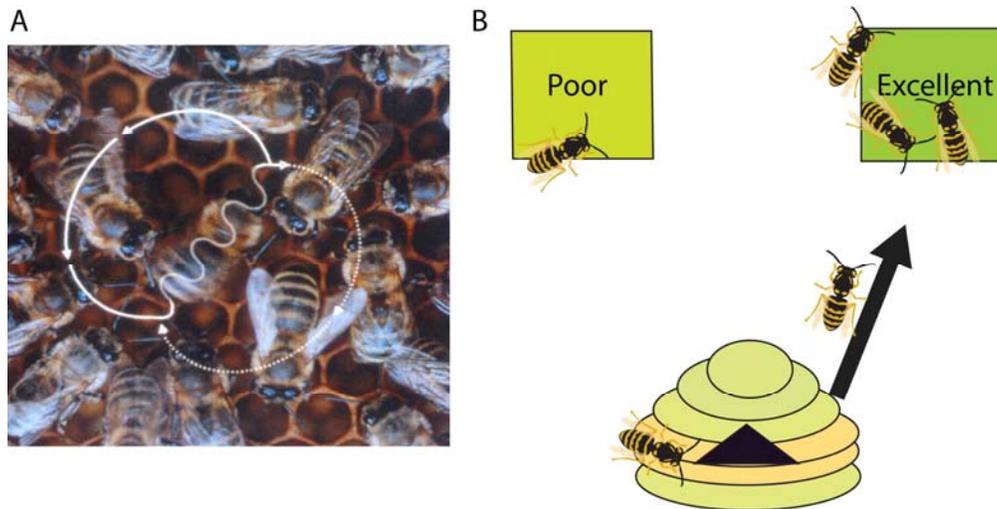
450

#### 451 **Conflict detection and resolution: honeybees**

452 Humans performing a cognitively demanding task may realize the task is harder  
453 than expected and devote more effort to it (Botvinick et al., 1999; Shenhav, Botvinick, &  
454 Cohen, 2013). For example, in the Stroop task, a subject is asked to either read a word or  
455 name the color of ink used to display it (Stroop, 1935). Reading the word is easy, but  
456 naming the ink color, especially when the word itself is a different color, requires more  
457 cognitive control. Another form of conflict is decisional conflict, which is caused by  
458 ambivalence between two equally desired options (Cai & Padoa-Schioppa, 2012 ;  
459 Hayden, Heilbronner, & Pearson, 2011; Strait, Blanchard, & Hayden, 2014; Amiez,  
460 Joseph, and Procyk, 2006). Modular models of conflict detection and resolution generally  
461 involve a discrete conflict detector and resolver, which are often located in the dorsal  
462 anterior cingulate cortex (dACC, Botvinick et al., 1999, Shenhav, Botvinick, & Cohen,  
463 2013; Botvinick et al., 2001). We hasten to note that such models, especially with regard  
464 to dACC, are contentious: the signal may not be conflict per se, but in either case, it may  
465 regulate control, which is our interest here (Kolling et al., 2016; Shenhav et al., 2016;  
466 Ebitz & Platt, 2015).

467 In springtime, thriving honeybee beehives reproduce. Roughly a third of the hive's  
468 members remain at the hive site and the others leave to form a swarm that gathers in one  
469 location and, in a few days, chooses a new hive site from a radius of several kilometers  
470 (Seeley, 2010; Seeley & Burhman, 1999; Camazine et al., 1999). Like our ants above,  
471 scouts evaluate promising nearby sites and then return and signal their quality with  
472 special dances (Figure 7). Dances indicating higher quality sites induce other bees to  
473 investigate the same site. When scouts detect a quorum of bees at a site (typically around  
474 20), they then return and provide a different signal, one that initiates a selection of the  
475 hive site by the swarm (Seeley, 2010; Seeley & Buhrman, 1999).

476



477  
478 *Figure 7. A) Image of honeybee waggle dance communication in a hive.*  
479 *Reproduced with permission from “Dances as a window into insect perception” (Chittka,*  
480 *2004). B) Illustration of binary choice between hive sites. Through quorum sensing by*  
481 *scouts at potential nest sites and waggle dance communication with the swarm, new*  
482 *hive locations are efficiently chosen.*  
483

484 If there is one obvious best site, the decision will proceed quickly. But if there are  
485 two or more sites of approximately equal quality, the decision will proceed more slowly  
486 as the bees take the time to choose the best one. The swarm therefore is sensitive to  
487 decisional conflict: it monitors its own level of decisional ambivalence as the decision  
488 proceeds. Note that this is conflict signal a swarm, not individual variable; after all, no  
489 bee knows about more than one site, so no bee is conflicted. By not halting the search  
490 process, the swarm effectively recruits more processing resources (i.e. more bee-search  
491 time) when conflict is high. As in mental effort, deliberation is not free; swarms are  
492 vulnerable to weather and predators so there is an opportunity cost to delaying the  
493 construction of the hive (Lindauer, 1957).

494 Notably, the detection and resolution of conflict are emergent phenomena. No  
495 single bee that is sensitive to the conflict level – we know the rules the bees follow and  
496 none of them deal with conflict. Nor is there a conflict signal represented in the bee’s  
497 waggle dance or at any other point in the system. No bee has a specialized role before the  
498 swarm starts swarming. Still, the swarm as a whole is quite sensitive to decisional  
499 conflict and able to deal with it efficiently. It’s also worth noting that an aggregate  
500 measure of hive activity, say, the number of active scouts or number of active dances  
501 during the decision, will show clear and strong aggregate conflict signals. This finding is  
502 intriguing because conflict signals are seldom observed in the activity of single neurons,  
503 and yet are robustly observed in the brain’s hemodynamic activity (see below).

504  
505  
506

#### Part IV. Evidence for distributed executive control in the brain

507 We turn now to the neuroscience of control. As noted above, there is a broad  
508 consensus that executive control is modular, not distributed (Botvinick & Cohen, 2014).  
509 We believe that one reason for relative unpopularity of distributed control systems by  
510 scholars is that they are unfamiliar and unintuitive. Indeed, distributed control is

511 notoriously difficult for us to intuit. Terms like the “ghost in the machine,” “the invisible  
512 hand of the marketplace,” “asking the hive mind” are reminders that our own minds  
513 naturally impute discrete and coherent agency even when dealing with mindless and  
514 ghostless distributed systems. Still, many distributed control systems are intuitive and can  
515 become more so with familiarity.

516

### 517 **Neuroscience methods make modularity easier to find**

518 Another factor disfavoring distributed control models is that the major methods for  
519 studying executive control, lesion, neuroimaging, and single unit recording, all arguably  
520 have some bias towards finding evidence of modularity.

521 Neuroimaging, like lesion studies, measures aggregate function of a given brain  
522 area or voxel, and thus cannot determine properties of the individual agents of the  
523 nervous system, neurons. This is true for multi-voxel pattern analysis as well as for ROI-  
524 type analyses. By aggregating signals across voxels, neuroimagers lose information  
525 about activity of individual neurons. The aggregate signal in turn misses information  
526 about the specific types of local, horizontal, and narrow-bandwidth signals that are  
527 crucial for distributed systems. But it is very good at detecting even weak signals at a  
528 broad range, meaning it can readily measure emergent properties of neural populations.  
529 The limitations of the lesion method are illustrated in a study by Plaut (1995). In this  
530 work, he shows how even the double dissociation, the gold standard of lesion studies, is  
531 susceptible to false positives supporting a modular view given certain reasonable  
532 assumptions about distributed network implementations of cognitive functions.

533 Single unit physiology studies are just as limited, although in the opposite way.  
534 Neurons may function much like agents, but the power of distributed systems comes in  
535 the specific local interactions of small numbers of agents. Physiology can measure the  
536 activity of only one neuron at a time; even multi-cellular methods have difficulty  
537 capturing interacting neurons. Moreover, most studies focus on a single brain region with  
538 the cost of inability to measure function at the level of the interregional network.

539 Historically, Karl Lashley had difficulty in finding the locus of memory function by  
540 lesion techniques (Lashley, 1929). This may have been because lesions to distributed  
541 systems do not selectively impair discrete functions, but instead have complex and  
542 unpredictable effects (Farah, 2004). Lashley found that degradation of behavioral  
543 performance depended on the amount of the brain regions removed independent of the  
544 precise location: they characteristically led to graceful degradation, which he interpreted  
545 as the product of mass action (Lashley, 1929). But when there is even a moderate amount  
546 of specialization in the system, they can lead to moderate but measurable effects. The  
547 interpretation of these effects, however, will be influenced by the experimenter’s  
548 theoretical framework.

549

### 550 **A case study: the dACC**

551 To look at these general issues in detail, we will take the dorsal anterior cingulate  
552 (dACC, often just ACC) as a case study. The dACC is part of the cingulum, a band of  
553 cortex that wraps around the corpus callosum in the sagittal plane. The dACC receives a  
554 broad and diverse set of inputs that includes both limbic and cognitive regions, as well as  
555 dopamine signals, and projects to motor, premotor, and executive regions. These factors  
556 make it a natural site for serving as a monitor and controller. Indeed, a great deal of

557 evidence links it to these two functions, among others. This evidence includes physiology  
558 (Heilbronner & Hayden, 2016), neuroimaging (Ridderinkoff et al., 2004; Shenhav,  
559 Botvinick, & Chohen, 2013; Kolling et al., 2012, Hare et al., 2011; Behrens et al., 2007;  
560 Hayden & Heilbronner, 2014), and lesion studies ( Rudebeck et al., 2006; Kennerley et  
561 al., 2006; Picton et al., 2007; Turken & Swick, 1999). Most prominently its responses are  
562 activated by contexts that promote control (Rushworth et al., 2011; Shenhav, Botvinick,  
563 & Cohen, 2013). These include conflict (Botvinick et al., 1999; Ebitz & Platt, 2015;  
564 Sheth et al., 2012; but see Kolling et al., 2016 and Ebitz & Hayden, 2016), surprising and  
565 unexpected outcomes (Matsumoto et al., 2007; Hayden et al., 2011; Ito et al., 2003),  
566 rewards (Seo & Lee, 2007; Hayden, Pearson, & Platt, 2009; Kennerley et al., 2009);  
567 progression through a task (Ma et al., 2014; Shidara & Richmond, 2002; Hayden,  
568 Pearson, & Platt, 2011b), changes in environmental context and volatility (Behrens et al.,  
569 2007; Procyk, Tanaka, & Joseph, 2000; Shima & Tanji, 1998), control of actions  
570 (Strait et al., 2016; Nakamura, Roesch, & Olson, 2005), and others not listed here. It is  
571 also directly activated by factors related to control, such as persistence (Blanchard, Strait,  
572 & Hayden, 2015; Chudasama et al., 2013; Parvizi et al., 2013; Hillman & Bilkey, 2012;  
573 Hillman & Bilkey, 2010).

574 These findings generally support a modular view of cognition, one in which dACC  
575 takes on the specialist role of monitor and controller. However, a broader review suggests  
576 that dACC is neither uniquely involved in monitoring and control, nor is its function  
577 primarily these two roles. Indeed, the very long list of functions above should raise  
578 suspicion for a devotee of the modular viewpoint. Yes, these variables can all be placed  
579 under the rubric of monitoring and control, but at some point the definition becomes so  
580 elastic that it contains almost all of cognition. Second, are all these functions found only  
581 in the dACC? Unlikely. Most of these functions are shared with many other brain regions  
582 (Cisek & Kalaska, 2010). For example, recent work points to the importance of the orbital  
583 surface in classically anterior cingulate functions like conflict monitoring and resolution  
584 (Mansouri, 2014), and regulating the explore-exploit tradeoff (Blanchard et al., 2015).

585 Studies that compare dACC activity with other brain regions often find that  
586 differences are more qualitative than quantitative (Hikosawa et al., 2013; Kennerley et  
587 al., 2009; Azab & Hayden, 2016). Indeed, control is associated with many other  
588 prefrontal structures, including OFC, dlPFC, vmPFC, and vlPFC (e.g. Schoenbaum et al.,  
589 2009; Wilson et al., 2014; Bechara, 2005; Buckley et al., 2009 ). Nor are these functions  
590 limited to the PFC; control signals are observed in the parietal cortex, the posterior  
591 cingulate cortex, the thalamus, and the striatum (e.g. Hayden, Smith, & Platt, 2010).

592 More broadly, summaries of dACC function tend to emphasize its potentially  
593 specialized role as a hub, linking visceral, cognitive, and motor systems (Bush, Luu,  
594 & Posner, 2000; Morecraft & VanHoesen, 1997; Rushworth et al., 2011; Paus, 2001;  
595 Heilbronner and Hayden, 2016). But is it really all that specialized? There is anatomical  
596 and functional evidence for its hub-nature, but it's also true of other brain regions,  
597 including, for example, PCC (Heilbronner, Hayden, & Platt, 2011; Heilbronner & Platt,  
598 2013) and insula. Indeed, rich interconnectivity is a feature of many brain systems (Wang  
599 & Kennedy, 2016; Heilbronner & Haber, 2014; Heilbronner et al., 2016).

600 Nor are the response properties observed in the dACC uniquely control-related.  
601 Many of them seem to fit naturally into the category of stimulus-response processing,  
602 rather than as a regulator of that processing. That is, if we think of the brain as a system

603 that converts sensory inputs to motor outputs, we should expect in a modular brain to find  
604 no sensory and motor signals in dACC, and instead find pure control-selective signals  
605 (Cisek, 2012). Instead, dACC is prominently responsive to both sensory stimuli and to  
606 actions. One convenient parameter to look at is spatial representation; this is a prominent  
607 property of the physical world but should, in theory, not be part of the recondite world of  
608 control. And yet dACC encodes the locations of stimuli under consideration and the  
609 specific details of actions (Hayden & Platt, 2010; Isomura et al., 2003; Luk & Wallis,  
610 2009; Stoll et al., 2016? ; Strait et al., 2016; Shima & Tanji, 1998).

611 Together these pieces of evidence argue that the differences between the dACC and  
612 adjacent structures are not as strong as is conventionally believed. They suggest instead a  
613 broad continuity of function between dACC and its neighbors and afferents. The broad  
614 functions, especially in the control domain, that it serves, are more distributed than  
615 modular. Moreover, the units of dACC – its neurons – appear to play a role in input-  
616 output processing as well as in generation of control signals. That is, from the perspective  
617 of a scientist accustomed to thinking about bee swarms and ant colonies, they look much  
618 like individual bugs: sensitive to multiple task parameters and capable of generating their  
619 own control signals, which influence their neighbors, and have the capability of  
620 participating in a larger cascade and, under the right circumstances, having effects at the  
621 aggregate level.

622

#### 623 **Maybe executive control could be distributed in the brain?**

624 A priori, it is not unreasonable to think so. A basic description of the brain sounds  
625 like an ideal candidate for a distributed control system. Neurons are agents that can only  
626 communicate with a very small number of neighbors relative to the whole population.  
627 Like bacteria, they use a variety of diffusible chemicals to communicate. Each neuron  
628 can monitor an extremely limited portion of the world and can broadcast its signals to a  
629 very narrow part of the world as well. Each neuron has limited but powerful and non-  
630 linear computational properties.

631 Moreover, each cell is autonomous, but they work together, non-competitively, in  
632 the service of a much larger goal (overcoming competition is a major barrier for many  
633 distributed systems, Sumpter, 2006). Individual neurons possess the ability to regulate the  
634 activity of other neurons (or output structures) through changes in firing rate. This  
635 activity can serve as both a processing and a regulatory role. The properties of the whole  
636 system (the brain) are rich and flexible, much more so than any of its constituents  
637 (Hofstadter, 1985, Ch. 26). The brain makes use of both positive and negative feedback,  
638 and shows slow changes over time.

639 Strong circumstantial evidence for the distributed view comes from lesion studies  
640 (Farah, 2004; Wilson et al., 2010). Damage has surprisingly weak and graded effects;  
641 graceful degradation is a well-known property of distributed systems (McClelland et al.,  
642 1987). Of the major “clean” effects associated with lesions (prosopagnosia, hemianopia,  
643 scotoma, and so on), few would be considered executive control effects. Instead,  
644 impairments in executive control can come from lesions in many different areas, and  
645 associated effects are generally graded, and only grow serious when the lesions become  
646 quite large (Farah, 2004; Lashley, 1929; Wilson et al., 2010).

647 Although there is some evidence for control-specific lesions (Shallice, 1982; Levine  
648 et al., 1998; Duncan et al., 1996), it may be difficult to pin these data clearly to control

649 functions. Instead, it may be that more difficult processing is impaired but simpler  
650 processing is spared. Consider, for example, an ant colony with a large proportion of  
651 members lesioned. That colony would have no trouble choosing a hive site if the decision  
652 was easy, but would have a great deal of trouble with a more difficult decision. We  
653 should not then conclude that the task-difficulty module is broken.

654 Indeed, the brain was the original inspiration for connectionist and PDP networks.  
655 The linkage between brain organization and other distributed control systems has been  
656 pointed out by many others before (Seeley, 2010; Couzin, 09; Passino et al., 2007;  
657 Mitchell, 2009). Given these facts, it is striking that the distributed view has not  
658 continued to serve as the null hypothesis for modular theories as a viable alternative  
659 view.

660

### 661 **Methods that can push for a distributed processing view**

662 However, recent technological advances have made the distributed processing  
663 more attractive for researchers. With the adoption of newer analysis techniques, a host of  
664 traditional imaging methodologies are beginning to highlight the interconnectivity and  
665 coordination of many brain regions during a variety of tasks (Sporns and Betzel, 2016).  
666 For example functional connectivity analysis is a growing trend in fMRI imaging studies  
667 (Sporns and Betzel, 2016; Craddock, Tungaraza, and Milham, 2015). In contrast to  
668 traditional ROI analysis, functional connectivity analysis focuses on the interaction  
669 pattern between the brain regions as the determinant of brain function rather than the  
670 activity of the single brain regions (Craddock, Tungaraza, and Milham, 2015; Sporns,  
671 Tononi, and Kotter, 2005). Likewise, an increasing emphasis on large-scale brain  
672 networks has lead to a revision of cognitive functions extending across modular  
673 boundaries and sparked efforts to define functional regions based on “connectional  
674 fingerprints” (Masic & Sporns, 2016; Passingham, Stephan, & Kotter, 2002). These  
675 trends have lead to the new field of network analysis and connectomics that emphasizes  
676 the interconnections of different brain regions across structure and function. A recurrent  
677 theme in many studies utilizing network analysis is the distributed processing nature  
678 inherent to many tasks across brain regions over a singular key region (Wang et al., 2015;  
679 Bressler & Menon, 2010).

680

### 681 **The modular vs. distributed debate in stopping and working memory**

682 For purposes of comparison, it is helpful to consider two aspects of executive  
683 control that have long been thought to be modular, but have more recently been  
684 challenged by a more distributed alternative view.

685 Influential work by Aron and others highlights the important and seemingly  
686 modular role of the right inferior frontal gyrus (rIFG) and anterior insula (aIns) in motor  
687 response inhibition, a form of executive control related to stopping (Rubia et al., 2001;  
688 Aron et al., 2003; Aron, Robbins, & Poldrack, 2004; Aron, Robbins, & Poldrack, 2014).  
689 However a recent series of studies challenges this view and proposes an alternative  
690 account that is more aligned with a distributed interpretation (Hampshire & Sharp, 2015;  
691 see also Munakata, 2011). Specifically, Hampshire and Sharp propose that stopping is the  
692 result of local processing by individual units that engage in lateral inhibition and  
693 potentiation, in a manner originally proposed for control of attention in the ventral stream  
694 (Desimone & Duncan, 1995; Chelazzi et al., 1998). In other words, they propose a simple

695 set of local rules that neuron/agents can follow and produce effective stopping behavior.  
696 This view implements classic stopping models and is consistent with relevant unit  
697 physiology – that is, with measures of the responses of the putative agents (Band et al.,  
698 2003; Boucher et al., 2007; Schall, Stuphorn, & Brown, 2002). In contrast to Aron and  
699 colleagues, they propose that the rIFG/aIns is part of a larger multiple demand cortex that  
700 flexibly handles many executive functions, including stopping (Duncan, 2001; Cole &  
701 Schneider, 2007; Erika-Florence, Leech, & Hampshire, 2014). Ultimately, they suggest  
702 that stopping may not be a valid psychological construct, but rather a term used to  
703 describe intuitively similar behaviors.

704 Another example comes from the domain of working memory. Classic  
705 neurophysiological works by Niki, Fuster and then Goldman-Rakic supported the idea  
706 that the DLPFC serves as the site of working memory storage (Kubota & Niki, 1971;  
707 Funahashi, Bruce, & Goldman-Rakic, 1989; Alexander & Fuster, 1971; reviewed in  
708 Riley & Constantinidis, 2016). The key evidence for this idea was the fact that single  
709 neurons in that region showed systematic changes associated with the contents of  
710 working memory. This is a modular view: it proposes that specific rostral regions serve  
711 as sites of storage for working memory, while posterior regions implement perception  
712 and association. A recent body of work challenges this view and argues for a more  
713 distributed alternative (reviewed in Postle, 2006; Pasternak & Greenlea, 2005; Postle,  
714 2016).

715 The alternative view proposes that neurons in frontal regions regulate storage  
716 (Lebedev et al., 2004; Postle, 2005), but that caudal regions responsible for perception  
717 are reactivated during working memory, and that their reactivation serves to store the  
718 information on-line (Harrison & Tong, 2009). This view thus sees perceptual neurons as  
719 flexible agents with multiple cognitive roles, including both basic processing and  
720 executive control roles. Indeed, further work suggests that modulations in these neurons  
721 may alter their responsiveness, thus serving as a form of proactive control that also  
722 implements memory-guided decisions (i.e. a matched filter, Machens, Romo, & Brody,  
723 2005; Miller & Wang, 2006; David et al., 2008; Jun & Romo, 2010; Mirabella et al.,  
724 2007; Hayden & Gallant, 2013; Ogawa & Komatsu, 2004).

725 Working memory is interesting to use because of its centrality in the history of  
726 modular theories (i.e. most theories) of executive control (Baddeley Hitch, 1974;  
727 Baddeley, 1996). Especially, the concept of the central executive, which supports the  
728 short-term memory in demanding tasks, has been thought to play a diverse control  
729 functions. However, subsequent studies discredited the general function of the central  
730 executive and rather fractionated its functions to number of the different operations  
731 (Logie, 2016). Thus, as a psychological construct, the concept of the central executive in  
732 working memory might no longer be regarded as the modular, centralized function and  
733 rather as the functions of the distributed nature.

734

735

## **CONCLUSIONS**

736

737 We do not mean to imply that no current work could be classified as distributed.  
738 Quite the opposite is true. Many models have distributed aspects (e.g. Botvinick et al.,  
739 2001; O'Reily, Herd, & Pauli, 2010; Behrman & Plaut, 2013; Botvinick & Plaut, 2004;  
740 Munakata et al., 2010; Botvinick & Plaut, 06; McClelland et al., 2010; Lenartowicz et al.,

741 2010). Instead, our major goals are to highlight the key distinguishing features of  
742 distributed and modular systems.

743

#### 744 **Advantages to a distributed control system**

745 From the perspective of adaptiveness, there are several advantages of a distributed  
746 control system with simple agents (Brooks & Flynn, 1989). First, because it is self-  
747 organized, there is no need to build a special centralized organization system that will  
748 link up control elements with their corresponding processors. A modular system requires  
749 the equivalent of a telephone switchboard; a distributed one does not. Second, that self-  
750 organization gets around the specter of infinite regress (Cooper, 2010). For example, if  
751 we have a special centralized organization system, we need another system to build and  
752 maintain it, and to monitor its functioning, and so on, ad infinitum. Self-organizing  
753 systems are easier developmentally – there is no need to pre-specify their organization  
754 genetically or any other way. They are also more robust to damage and can more readily  
755 adapt and be amenable to plasticity, such as occurs with learning. They are generally  
756 more flexible for novel situations. Finally, and most important, distributed control is a  
757 good way to get complex and adaptive behavior from systems consisting of elements that  
758 are less complex (Sumpter, 2006). From a theoretical perspective, distributed system  
759 makes sense. Many brain functions are distributed, including perception and object  
760 recognition, storage of episodic memories, motor planning and execution, and, arguably,  
761 economic decision-making (Strait, Sleezer, & Hayden, 2015; Cisek, 2012; Cisek &  
762 Kalaska, 2010).

763

#### 764 **How to study distributed executive control systems**

765 Distributed control systems may be more difficult to study than modular ones  
766 with conventional methods. In many studies (including, we hasten to admit, many of our  
767 own), we pick out some psychological process of interest. We then ask whether brain  
768 activity in some neuron or voxel within a given brain region correlates with a measure of  
769 that variable. If we get a positive result, the simplest step is to infer that that variable is  
770 reified in the brain. The distributed perspective cautions against this strategy; such  
771 correlations may be real, but may only correlate with emergent properties of the system.  
772 And if the underlying processes are dissimilar, we will draw false conclusions. In other  
773 words, we are always in danger of reifying higher level processes at the lower level.

774 Instead, the best strategy for dealing with this possibility is a top-down research  
775 program. We should come up with specific hypotheses about how distributed control  
776 systems might work, and then estimate its expected neural signatures (e.g. Hampshire &  
777 Sharp, 2015). The next step is to identify the results expected from alternative distributed  
778 or even modular implementations, and perform the critical test of comparing alternative  
779 views. This approach is agnostic about method; it can be applied to unit physiology,  
780 neuroimaging, or even reaction times (Louie, Kaw, & Glimcher, 2013; Chau et al., 2014).  
781 And it's worth reiterating that the two modular and the distributed views are not mutually  
782 incompatible. In reality, they may exist on a spectrum. And executive control may be  
783 heterogeneous; some aspects may be modular while others may be distributed.

784 The relevant hypotheses will come, as always, from close consideration of the  
785 data; especially from attempts to interpret data that conflict with preconceptions. But  
786 also, they can come from the animal kingdom, as we have discussed in this review.

787 Brains are complex distributed systems, and they face many of the same constraints as  
788 others. It should not be surprising that they have a great deal in common with ant  
789 colonies, bee swarms, and herds of migrating baboons (Couzin, 2009; Sumpter, 2006;  
790 Passino et al., 2007; Seeley, 2010; Hofstadter, 1980; Hofstadter, 1985, Ch. 25, 26).  
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## REFERENCES

- Afek, Y., Alon, N., Barad, O., Hornstein, E., Barkai, N., & Bar-Joseph, Z. (2011). A biological solution to a fundamental distributed computing problem. *Science* 331: 183-185.
- Aoki, I. (1982) A simulation study on the schooling mechanism in fish. *Bulletin of the Japanese Society of Scientific Fisheries*. 48:1081-1088.
- Aron, A. R., Fletcher, P. C., Bullmore, E. T., Sahakian, B. J., & Robbins, T. W. (2003). Stop-signal inhibition disrupted by damage to right inferior frontal gyrus in humans. *Nature neuroscience*, 6(2), 115-116.
- Aron, A. R., Robbins, T. W., & Poldrack, R. A. (2004). Inhibition and the right inferior frontal cortex. *Trends in cognitive sciences*, 8(4), 170-177.
- Aron, A. R., & Poldrack, R. A. (2006). Cortical and subcortical contributions to stop signal response inhibition: role of the subthalamic nucleus. *The Journal of Neuroscience*, 26(9), 2424-2433.
- Aron, A.R., Robbins, T.W., & Poldrack, R.A. (2014). Inhibition and the right inferior frontal cortex: one decade on. *Trends Cogn Sci* 18:177–185.
- Aron, S., Beckers, R., Deneubourg, J. L., & Pasteels, J. M. (1993). Memory and chemical communication in the orientation of two mass-recruiting ant species. *Insectes Sociaux*, 40(4), 369-380.
- Awh, E., & Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. *Trends in Cognitive Sciences*. 5:119-126.
- Azab, H., & Hayden, B.Y. (2016). Shared roles of dorsal and subgenual anterior cingulate cortices in economic decisions. *BioRxiv*. 074484.
- Baddeley, A.D., & Hitch, G. (1974). Working Memory. In: *Psychology of Learning and Motivation* (Bower GH, ed), pp 47–89. Academic Press. Available at: <http://www.sciencedirect.com/science/article/pii/S0079742108604521> [Accessed August 12, 2016].
- Baddeley, A. (1996). Exploring the central executive. *The Quarterly Journal of Experimental Psychology: Section A*, 49(1), 5-28.
- Band, G. P., Van Der Molen, M. W., & Logan, G. D. (2003). Horse-race model simulations of the stop-signal procedure. *Acta psychologica*, 112(2), 105-142.
- Bechara, A. (2005). Decision making, impulse control and loss of willpower to resist drugs: a neurocognitive perspective. *Nature neuroscience*, 8(11), 1458-1463.
- Beckers, R., Deneubourg, J. L., & Goss, S. (1992). Trails and U-turns in the selection of a path by the ant *Lasius niger*. *Journal of theoretical biology*, 159(4), 397-415.
- Beekman, M., Sumpter, D. J., & Ratnieks, F. L. (2001). Phase transition between disordered and ordered foraging in Pharaoh's ants. *Proceedings of the National Academy of Sciences*, 98(17), 9703-9706.

- Behrens, T. E., Woolrich, M. W., Walton, M. E., & Rushworth, M. F. (2007). Learning the value of information in an uncertain world. *Nature neuroscience*, *10*(9), 1214-1221.
- Behrmann, M., & Plaut, D. C. (2013). Distributed circuits, not circumscribed centers, mediate visual recognition. *Trends in cognitive sciences*, *17*(5), 210-219.
- Bergman, G., & Donner, K. O. (1964). An analysis of the spring migration of the common scoter and the long-tailed duck in southern Finland. *Acta Zool Fenn.* 105:1-59.
- Bertolero, M.A., Yeo, B.T.T., & D'Esposito, M. (2015). The modular and integrative functional architecture of the human brain. *Proc Natl Acad Sci* 112:E6798–E6807.
- Biro, D., Sumpter, D. J., Meade, J., & Guilford, T. (2006). From compromise to leadership in pigeon homing. *Current Biology*, *16*(21), 2123-2128.
- Blanchard, T.C., Hayden, B.Y., & Bromberg-Martin, E.S. (2015). Orbitofrontal Cortex Uses Distinct Codes for Different Choice Attributes in Decisions Motivated by Curiosity. *Neuron* 85:602–614.
- Blanchard, T. C., Strait, C. E., & Hayden, B. Y. (2015). Ramping ensemble activity in dorsal anterior cingulate neurons during persistent commitment to a decision. *Journal of neurophysiology*, *114*(4), 2439-2449.
- Bogacz, R., Wagenmakers, E. J., Forstmann, B. U., & Nieuwenhuis, S. (2010). The neural basis of the speed–accuracy tradeoff. *Trends in neurosciences*, *33*(1), 10-16.
- Bonabeau, E., Dorigo, M., & Theraulaz, G. (1999). *Swarm intelligence: from natural to artificial systems* (No. 1). Oxford university press.
- Botvinick, M., Nystrom, L. E., Fissell, K., Carter, C. S., & Cohen, J. D. (1999). Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature*, *402*(6758), 179-181.
- Botvinick, M.M., Braver, T.S., Barch, D.M., Carter, C.S., & Cohen, J.D. (2001). Conflict monitoring and cognitive control. *Psychol Rev* 108:624–652.
- Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Evaluating the demand for control: Anterior cingulate cortex and conflict monitoring. *Psychological Review*, *108*(3), 624-652.
- Botvinick, M. M., Cohen, J. D., & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: an update. *Trends in cognitive sciences*, *8*(12), 539-546.
- Botvinick, M. M., & Cohen, J. D. (2014). The computational and neural basis of cognitive control: charted territory and new frontiers. *Cognitive science*, *38*(6), 1249-1285.
- Botvinick, M., & Plaut, D. C. (2004). Doing without schema hierarchies: a recurrent connectionist approach to normal and impaired routine sequential action. *Psychological review*, *111*(2), 395.

- Botvinick, M. M., & Plaut, D. C. (2006). Short-term memory for serial order: a recurrent neural network model. *Psychological review*, *113*(2), 201.
- Boucher, L., Palmeri, T. J., Logan, G. D., & Schall, J. D. (2007). Inhibitory control in mind and brain: an interactive race model of countermanding saccades. *Psychological review*, *114*(2), 376.
- Braver, T.S., & Barch, D.M. (2006). Extracting core components of cognitive control. *Trends Cogn Sci* 10:529–532.
- Bressler, S.L., & Menon, V. (2010). Large-scale brain networks in cognition: emerging methods and principles. *Trends in Cognitive Sciences* 14:277-290.
- Brooks, R. A., & Flynn, A. M. (1989). *Fast, cheap and out of control* (No. AI-M-1182). Massachusetts Inst of Tech Cambridge Artificial Intelligence Lab.
- Buckley, M. J., Mansouri, F. A., Hoda, H., Mahboubi, M., Browning, P. G., Kwok, S. C., ... & Tanaka, K. (2009). Dissociable components of rule-guided behavior depend on distinct medial and prefrontal regions. *Science*, *325*(5936), 52-58.
- Busemeyer, J. R., & Townsend, J. T. (1993). Decision field theory: a dynamic-cognitive approach to decision making in an uncertain environment. *Psychological review*, *100*(3), 432.
- Bush, G., Luu, P., & Posner, M. I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in cognitive sciences*, *4*(6), 215-222.
- Cai, X., & Padoa-Schioppa, C. (2012). Neuronal encoding of subjective value in dorsal and ventral anterior cingulate cortex. *The Journal of Neuroscience*, *32*(11), 3791-3808.
- Camazine, S., Visscher, P. K., Finley, J., & Vetter, R. S. (1999). House-hunting by honey bee swarms: collective decisions and individual behaviors. *Insectes Sociaux*, *46*(4), 348-360.
- Cisek, P., & Kalaska, J. F. (2010). Neural mechanisms for interacting with a world full of action choices. *Annual review of neuroscience*, *33*, 269-298.
- Cisek, P. (2012). Making decisions through a distributed consensus. *Current opinion in neurobiology*, *22*(6), 927-936.
- Chafee, M.V., & Goldman-Rakic, P.S. (1998). Matching Patterns of Activity in Primate Prefrontal Area 8a and Parietal Area 7ip Neurons During a Spatial Working Memory Task. *J Neurophysiol* 79:2919–2940.
- Chau, B. K., Kolling, N., Hunt, L. T., Walton, M. E., & Rushworth, M. F. (2014). A neural mechanism underlying failure of optimal choice with multiple alternatives. *Nature neuroscience*, *17*(3), 463-470.
- Chelazzi, L., Duncan, J., Miller, E. K., & Desimone, R. (1998). Responses of neurons in inferior temporal cortex during memory-guided visual search. *Journal of neurophysiology*, *80*(6), 2918-2940.
- Chittka, L., Dyer, A. G., Bock, F., & Dornhaus, A. (2003). Psychophysics: bees trade off foraging speed for accuracy. *Nature*, *424*(6947), 388-388.

- Chittka, L. (2004). Dances as windows into insect perception. *PLoS Biol*, 2(7), e216.
- Chittka, L., Skorupski, P., & Raine, N. E. (2009). Speed–accuracy tradeoffs in animal decision making. *Trends in Ecology & Evolution*, 24(7), 400-407.
- Chudasama, Y., Daniels, T.E., Gorrin, D.P., Rhodes, S.E.V., Rudebeck, P.H., & Murray, E.A. (2013). The role of the anterior cingulate cortex in choices based on reward value and reward contingency. *Cerebral Cortex*. 23:2884-2899.
- Codling, E. A., Pitchford, J. W., & Simpson, S. D. (2007). Group navigation and the "many-wrongs principle" in models of animal movement. *Ecology*, 88(7), 1864-1870.
- Cole, M.W., & Schneider, W. (2007). The cognitive control network: Integrated cortical regions with dissociable functions. *NeuroImage* 37:343–360.
- Conradt, L., & Roper, T. J. (2003). Group decision-making in animals. *Nature*, 421(6919), 155-158.
- Cooper, R. P. (2010). Cognitive control: componential or emergent?. *Topics in Cognitive Science*, 2(4), 598-613.
- Couzin, I. D., & Krause, J. (2003). Self-organization and collective behavior in vertebrates. *Advances in the Study of Behavior*, 32, 1-75.
- Couzin, I. D. (2009). Collective cognition in animal groups. *Trends in cognitive sciences*, 13(1), 36-43.
- Couzin, I. D., Krause, J., James, R., Ruxton, G. D., & Franks, N. R. (2002). Collective memory and spatial sorting in animal groups. *Journal of theoretical biology*, 218(1), 1-11.
- Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature*, 433(7025), 513-516.
- Craddock, R.C., Tungaraza, R.L., & Milham, M.P. (2015). Connectomics and new approaches for analyzing human brain functional connectivity. 4:13-25.
- David, S. V., Hayden, B. Y., Mazer, J. A., & Gallant, J. L. (2008). Attention to stimulus features shifts spectral tuning of V4 neurons during natural vision. *Neuron*, 59(3), 509-521.
- Daw, N.D., O’Doherty, J.P., Dayan, P., Seymour, B., & Dolan, R.J. (2006). Cortical substrates for exploratory decisions in humans. *Nature* 441:876–879.
- Delsuc, F. (2003). Army ants trapped by their evolutionary history. *PLoS Biol*, 1(2), e37.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual review of neuroscience*, 18(1), 193-222.
- Duncan, J. (2001). An adaptive coding model of neural function in prefrontal cortex. *Nature Reviews Neuroscience*, 2(11), 820-829.
- Duncan, J., Emslie, H., Williams, P., Johnson, R., & Freer, C. (1996). Intelligence and the frontal lobe: The organization of goal-directed behavior. *Cognitive psychology*, 30(3), 257-303.

- Dussutour, A., Latty, T., Beekman, M., & Simpson, S. J. (2010). Amoeboid organism solves complex nutritional challenges. *Proceedings of the National Academy of Sciences*, *107*(10), 4607-4611.
- Dyer, J. R., Ioannou, C. C., Morrell, L. J., Croft, D. P., Couzin, I. D., Waters, D. A., & Krause, J. (2008). Consensus decision making in human crowds. *Animal Behaviour*, *75*(2), 461-470.
- Ebitz, R.B., & Platt, M.L. (2015). Neuronal Activity in primate dorsal anterior cingulate cortex signals task conflict and predicts adjustments in pupil-linked arousal. *Neuron*. *85*: 628-640.
- Ebitz, R.B., & Hayden, B.Y. (2016). Dorsal anterior cingulate: a rorschach test for cognitive neuroscience. *Nature Neuroscience*. *19*:1-3.
- Erika-Florence, M., Leech, R., & Hampshire, A. (2014). A functional network perspective on response inhibition and attentional control. *Nature communications*, *5*.
- Farah, M. J. (1994). Neuropsychological inference with an interactive brain: A critique of the “locality” assumption. *Behavioral and Brain Sciences*, *17*(01), 43-61.
- Fischhoff, I. R., Sundaresan, S. R., Cordingley, J., Larkin, H. M., Sellier, M. J., & Rubenstein, D. I. (2007). Social relationships and reproductive state influence leadership roles in movements of plains zebra, *Equus burchellii*. *Animal Behaviour*, *73*(5), 825-831.
- Floresco, S. B. (2015). The nucleus accumbens: an interface between cognition, emotion, and action. *Annual review of psychology*, *66*, 25-52.
- Fodor, J.A. (1983). *The Modularity of Mind: An Essay on Faculty Psychology*. MIT Press.
- Frank, M. J., Scheres, A., & Sherman, S. J. (2007). Understanding decision-making deficits in neurological conditions: insights from models of natural action selection. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *362*(1485), 1641-1654.
- Franks, N. R., Pratt, S. C., Mallon, E. B., Britton, N. F., & Sumpter, D. J. (2002). Information flow, opinion polling and collective intelligence in house-hunting social insects. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *357*(1427), 1567-1583.
- Franks, N. R., Dornhaus, A., Fitzsimmons, J. P., & Stevens, M. (2003). Speed versus accuracy in collective decision making. *Proceedings of the Royal Society of London B: Biological Sciences*, *270*(1532), 2457-2463.
- Forstmann, B. U., Dutilh, G., Brown, S., Neumann, J., Von Cramon, D. Y., Ridderinkhof, K. R., & Wagenmakers, E. J. (2008). Striatum and pre-SMA facilitate decision-making under time pressure. *Proceedings of the National Academy of Sciences*, *105*(45), 17538-17542.

- Funahashi, S., Bruce, C. J., & Goldman-Rakic, P. S. (1989). Mnemonic coding of visual space in the monkey's dorsolateral prefrontal cortex. *Journal of neurophysiology*, *61*(2), 331-349.
- Fuster, J. M., & Alexander, G. E. (1971). Neuron activity related to short-term memory. *Science*, *173*(3997), 652-654.
- Gallistel, C. R. (2013). *The organization of action: A new synthesis*. Psychology Press.
- Gigerenzer, G., & Goldstein, D. G. (1996). Reasoning the fast and frugal way: models of bounded rationality. *Psychological review*, *103*(4), 650.
- Giraldeau, L. A., Valone, T. J., & Templeton, J. J. (2002). Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *357*(1427), 1559-1566.
- Grossberg, S. (1974). Classical and instrumental learning by neural networks. *Prog Theor Biol* *3*:42-47.
- Grünbaum, D. (1998). Schooling as a strategy for taxis in a noisy environment. *Evolutionary Ecology*, *12*(5), 503-522.
- Hamilton, W.J. (1967). Social aspects of bird orientation mechanisms. In *Animal Orientation and Navigation*. Storm, RM ed., 57-71, Oregon State University Press.
- Hampshire, A., & Sharp, D. J. (2015). Contrasting network and modular perspectives on inhibitory control. *Trends in cognitive sciences*, *19*(8), 445-452.
- Hare, T.A., Camerer, C.F., Rangel, A. (2009). Self-Control in Decision-Making Involves Modulation of the vmPFC Valuation System. *Science* *324*:646-648.
- Hare, T.A., Schultz, W., Camerer, C.F., O'Doherty, J.P., & Rangel, A. (2011). Transformation of stimulus value signals into motor commands during simple choice. *Proc. Natl. Acad. Sci.* *108*:18120-18125.
- Harrison, S. A., & Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. *Nature*, *458*(7238), 632-635.
- Hayden, B.Y., Nair, A.C., McCoy, A.N., Platt, M.L. (2008). Posterior cingulate cortex mediates outcome-contingent allocation of behavior. *Neuron*. *60*:19-25.
- Hayden, B. Y., Pearson, J. M., & Platt, M. L. (2009). Fictive reward signals in the anterior cingulate cortex. *science*, *324*(5929), 948-950.
- Hayden, B. Y., & Platt, M. L. (2010). Neurons in anterior cingulate cortex multiplex information about reward and action. *The Journal of Neuroscience*, *30*(9), 3339-3346.
- Hayden, B., Smith, D. V., & Platt, M. (2010). Cognitive control signals in posterior cingulate cortex. *Frontiers in human neuroscience*, *4*, 223.
- Hayden, B. Y., Heilbronner, S. R., Pearson, J. M., & Platt, M. L. (2011). Surprise signals in anterior cingulate cortex: neuronal encoding of unsigned reward prediction errors driving adjustment in behavior. *The Journal of Neuroscience*, *31*(11), 4178-4187.

- Hayden, B. Y., Pearson, J. M., & Platt, M. L. (2011). Neuronal basis of sequential foraging decisions in a patchy environment. *Nature neuroscience*, *14*(7), 933-939.
- Hayden, B.Y., Heilbronner, S.R. (2014). All that glitters is not reward signal. *Nature Neuroscience*. *17*:1142-1144.
- Hayden, B.Y., & Gallant, J. (2013). Working memory and decision processes in visual area v4. *Frontiers in neuroscience*, *7*, 18.
- Heilbronner, S., Hayden, B. Y., & Platt, M. (2011). Decision salience signals in posterior cingulate cortex. *Frontiers in neuroscience*, *5*, 55.
- Heilbronner, S. R., & Haber, S. N. (2014). Frontal cortical and subcortical projections provide a basis for segmenting the cingulum bundle: implications for neuroimaging and psychiatric disorders. *The Journal of Neuroscience*, *34*(30), 10041-10054.
- Heilbronner, S.R., & Platt, M.L. (2013). Causal evidence of performance monitoring by neurons in posterior cingulate cortex during learning. *Neuron*. *80*:1384-1391.
- Heilbronner, S. R., & Hayden, B. Y. (2016). Dorsal Anterior Cingulate Cortex: A Bottom-Up View. *Annual review of neuroscience*.
- Heilbronner, S. R., Rodriguez-Romaguera, J., Quirk, G. J., Groenewegen, H. J., & Haber, S. N. (2016). Circuit Based Cortico-Striatal Homologies between Rat and Primate. *Biological Psychiatry*.
- Helbing, D., Keltsch, J., & Molnar, P. (1997). Modelling the evolution of human trail systems. *Nature*, *388*(6637), 47-50.
- Hernández, A., Nácher, V., Luna, R., Zainos, A., Lemus, L., Alvarez, M., Vázquez, Y., Camarillo, L., & Romo, R. (2010). Decoding a Perceptual Decision Process across Cortex. *Neuron* *66*:300–314.
- Hillman, K.L., Bilkey, D.K. (2010). Neurons in the rat anterior cingulate cortex dynamically encode cost-benefit in a spatial decision-making task. *Journal of Neuroscience*. *30*:7705-7713.
- Hillman, K.L., Bilkey, D.K. (2012). Neural encoding of competitive effort in the anterior cingulate cortex. *Nature Neuroscience*. *9*:1290-1298.
- Hinton, G. E., & Salakhutdinov, R. R. (2006). Reducing the dimensionality of data with neural networks. *Science*, *313*(5786), 504-507.
- Hofstadter, D. R. (1980). Godel, Escher, Bach. *New Society*.
- Hofstadter, DR. (1985). Who shoves whom around inside the careenium? or, what is the meaning of the word "I". In Hofstadter, D.R. *Metamagical themas: Questing for the essence of mind and pattern*. (chapter 25). Basic books.
- Hofstadter, DR. (1985). Waking up from the boolean dream, or subcognition as computation. In Hofstadter, D.R. *Metamagical themas: Questing for the essence of mind and pattern*. (chapter 26). Basic books.

- Hosokawa, T., Kennerley, S. W., Sloan, J., & Wallis, J. D. (2013). Single-neuron mechanisms underlying cost-benefit analysis in frontal cortex. *The Journal of Neuroscience*, *33*(44), 17385-17397.
- Hölldobler, B., & Wilson, E. O. (1990). *The ants*. Harvard University Press.
- Holroyd, C. B., & Coles, M. G. (2002). The neural basis of human error processing: reinforcement learning, dopamine, and the error-related negativity. *Psychological review*, *109*(4), 679.
- Hopfield, J.J. (1982). Neural networks and physical systems with emergent collective computational abilities. *Proc Natl Acad Sci* *79*:2554–2558.
- Houston, A. I., Kacelnik, A., & McNamara, J. O. H. N. (1982). Some learning rules for acquiring information. *Functional ontogeny*, *1*, 140-191.
- Ito, S., Stuphorn, V., Brown, J. W., & Schall, J. D. (2003). Performance monitoring by the anterior cingulate cortex during saccade countermanding. *Science*, *302*(5642), 120-122.
- Ivanoff, J., Branning, P., & Marois, R. (2008). fMRI evidence for a dual process account of the speed-accuracy tradeoff in decision-making. *PLoS one*, *3*(7), e2635.
- Isomura, Y., Ito, Y., Akazawa, T., Nambu, A., & Takada, M. (2003). Neural coding of “attention for action” and “response selection” in primate anterior cingulate cortex. *The Journal of neuroscience*, *23*(22), 8002-8012.
- Jackson, D. E., & Châline, N. (2007). Modulation of pheromone trail strength with food quality in Pharaoh's ant, *Monomorium pharaonis*. *Animal behaviour*, *74*(3), 463-470.
- Jin, X., & Costa, R. M. (2010). Start/stop signals emerge in nigrostriatal circuits during sequence learning. *Nature*, *466*(7305), 457-462.
- Jun, J. K., Miller, P., Hernández, A., Zainos, A., Lemus, L., Brody, C. D., & Romo, R. (2010). Heterogenous population coding of a short-term memory and decision task. *The Journal of Neuroscience*, *30*(3), 916-929.
- Kacelnik, A., Vasconcelos, M., Monteiro, T., & Aw, J. (2011). Darwin's “tug-of-war” vs. starlings' “horse-racing”: how adaptations for sequential encounters drive simultaneous choice. *Behavioral Ecology and Sociobiology*, *65*(3), 547-558.
- Kalivas, P.W., Volkow, N.D. (2005). The neural basis of addiction: a pathology of motivation and choice. *American Journal of Psychiatry*. *162*:1403-1413.
- Kanwisher, N., McDermott, J., & Chun, M.M. (1997). The Fusiform Face Area: A Module in Human Extrastriate Cortex Specialized for Face Perception. *J Neurosci* *17*:4302–4311.
- Kaplan, H. B., & Greenberg, E. P. (1985). Diffusion of autoinducer is involved in regulation of the *Vibrio fischeri* luminescence system. *Journal of bacteriology*, *163*(3), 1210-1214.

- Kennerley, S. W., Walton, M. E., Behrens, T. E., Buckley, M. J., & Rushworth, M. F. (2006). Optimal decision making and the anterior cingulate cortex. *Nature neuroscience*, 9(7), 940-947.
- Kennerley, S. W., Dahmubed, A. F., Lara, A. H., & Wallis, J. D. (2009). Neurons in the frontal lobe encode the value of multiple decision variables. *Journal of cognitive neuroscience*, 21(6), 1162-1178.
- Kidd, C., & Hayden, B.Y. (2015). The psychology and neuroscience of curiosity. *Neuron* 88:449–460.
- Kim, J.N., & Shadlen, M.N. (1999). Neural correlates of a decision in the dorsolateral prefrontal cortex of the macaque. *Nat Neurosci* 2:176–185.
- Kolling, N., Behrens, T.E.J., Mars, R.B., & Rushworth, M.F.S. (2012) Neural mechanisms of foraging. *Science*. 336:95-98.
- Kolling, N., Behrens, T. E. J., Wittmann, M. K., & Rushworth, M. F. S. (2016). Multiple signals in anterior cingulate cortex. *Current opinion in neurobiology*, 37, 36-43.
- Knoch, D., & Fehr, E. (2007). Resisting the Power of Temptations. *Ann N Y Acad Sci* 1104:123–134.
- Kristan, W.B., & Shaw, BK. (1997). Population coding and behavioral choice. *Current Opinion in Neurobiology*. 7:826-831.
- Kubota, K., & Niki, H. (1971). Prefrontal cortical unit activity and delayed alternation performance in monkeys. *Journal of Neurophysiology*.
- Lashley, K. (1951). The problem of serial order in behavior. In: *Cerebral mechanisms in behavior; the Hixon Symposium*, pp 112–146. Oxford, England: Wiley.
- LeCun, Y., Bengio, Y., & Hinton, G. (2015). Deep learning. *Nature*, 521(7553), 436-444.
- Lebedev, M. A., Messinger, A., Kralik, J. D., & Wise, S. P. (2004). Representation of attended versus remembered locations in prefrontal cortex. *PLoS Biol*, 2(11), e365.
- Lenartowicz, A., Kalar, D. J., Congdon, E., & Poldrack, R. A. (2010). Towards an ontology of cognitive control. *Topics in Cognitive Science*, 2(4), 678-692.
- Levine, B., Stuss, D. T., Milberg, W. P., Alexander, M. P., Schwartz, M., & MacDonald, R. (1998). The effects of focal and diffuse brain damage on strategy application: Evidence from focal lesions, traumatic brain injury and normal aging. *Journal of the International Neuropsychological Society*, 4(03), 247-264.
- Lindauer, M. (1957). Communication among the honeybees and stingless bees of India. *Bee World*, 38(1), 3-14.
- Logie, R. H. (2016). Retiring the central executive. *The Quarterly Journal of Experimental Psychology*, 1-17.
- Louie, K., Khaw, M. W., & Glimcher, P. W. (2013). Normalization is a general neural mechanism for context-dependent decision making. *Proceedings of the National Academy of Sciences*, 110(15), 6139-6144.

- Luk, C. H., & Wallis, J. D. (2009). Dynamic encoding of responses and outcomes by neurons in medial prefrontal cortex. *The Journal of Neuroscience*, 29(23), 7526-7539.
- Ma, L., Hyman, J. M., Phillips, A. G., & Seamans, J. K. (2014). Tracking progress toward a goal in corticostriatal ensembles. *The Journal of Neuroscience*, 34(6), 2244-2253.
- Machens, C. K., Romo, R., & Brody, C. D. (2005). Flexible control of mutual inhibition: a neural model of two-interval discrimination. *Science*, 307(5712), 1121-1124.
- Mallon, E., Pratt, S., & Franks, N. (2001). Individual and collective decision-making during nest site selection by the ant *Leptothorax albipennis*. *Behavioral Ecology and Sociobiology*, 50(4), 352-359.
- Mansouri, F. A., Buckley, M. J., & Tanaka, K. (2007). Mnemonic function of the dorsolateral prefrontal cortex in conflict-induced behavioral adjustment. *Science*, 318(5852), 987-990.
- Matsumoto, M., Matsumoto, K., Abe, H., & Tanaka, K. (2007). Medial prefrontal cell activity signaling prediction errors of action values. *Nature Neuroscience*. 10:647-658.
- McFall-Ngai, M. (2014). Divining the essence of symbiosis: insights from the squid-vibrio model. *PLoS Biol*, 12(2), e1001783.
- Milad, M.R., Rauch, S.L. (2012). Obsessive-compulsive disorder: beyond segregated cortico-striatal pathways. *Trends in cognitive science*. 16:43-52.
- Miller, P., & Wang, X. J. (2006). Inhibitory control by an integral feedback signal in prefrontal cortex: a model of discrimination between sequential stimuli. *Proceedings of the National Academy of Sciences of the United States of America*, 103(1), 201-206.
- Mirabella, G., Bertini, G., Samengo, I., Kilavik, B. E., Frilli, D., Della Libera, C., & Chelazzi, L. (2007). Neurons in area V4 of the macaque translate attended visual features into behaviorally relevant categories. *Neuron*, 54(2), 303-318.
- McClelland, J. L., Rumelhart, D. E., & PDP Research Group. (1987). *Parallel distributed processing* (Vol. 2). Cambridge, MA: MIT press.
- McClelland, J.L., Botvinick, M.M., Noelle, D.C., Plaut, D.C., Rogers, T.T., Seidenberg, M.S., & Smith, L.B. (2010). Letting structure emerge: connectionist and dynamical systems approaches to cognition. *Trends Cogn Sci* 14:348–356.
- Miller, E.K. (2000). The prefrontal cortex and cognitive control. *Nat Rev Neurosci* 1:59–65.
- Miller, E.K., & Cohen, J.D. (2001). An Integrative Theory of Prefrontal Cortex Function. *Annu Rev Neurosci* 24:167–202.
- Miller, M. B., & Bassler, B. L. (2001). Quorum sensing in bacteria. *Annual Reviews in Microbiology*, 55(1), 165-199.

- Misic, B., & Sporns, O. (2016). From regions to connections and networks: new bridges between brain and behavior. *Current Opinion in Neurobiology* 40:1-7
- Minsky, M. (1988). *Society of mind*. Simon and Schuster.
- Mitchell, M. (2009). *Complexity: A guided tour*. Oxford University Press.
- Morecraft, R.J., & Van Hoesen, G.W. (1997). Convergence of limbic input to the cingulate motor cortex in the rhesus monkey. *Brain Research Bulletin*. 45:209-232.
- Munakata, Y., Herd, S. A., Chatham, C. H., Depue, B. E., Banich, M. T., & O'Reilly, R. C. (2011). A unified framework for inhibitory control. *Trends in cognitive sciences*, 15(10), 453-459.
- Nakamura, K., Roesch, M. R., & Olson, C. R. (2005). Neuronal activity in macaque SEF and ACC during performance of tasks involving conflict. *Journal of neurophysiology*, 93(2), 884-908.
- Navlakha, S., & Bar-Joseph, Z. (2011). Algorithms in nature: the convergence of systems biology and computational thinking. *Molecular Systems Biology*7: 546-557.
- Néda, Z., Ravasz, E., Brechet, Y., Vicsek, T., & Barabási, A. L. (2000). Self-organizing processes: The sound of many hands clapping. *Nature*, 403(6772), 849-850.
- Nealson, K. H., & Hastings, J. W. (1979). Bacterial bioluminescence: its control and ecological significance. *Microbiological reviews*, 43(4), 496.
- Niv, Y., Daw, N. D., Joel, D., & Dayan, P. (2007). Tonic dopamine: opportunity costs and the control of response vigor. *Psychopharmacology*, 191(3), 507-520.
- Norman, D.A., & Shallice, T. (1986). Attention to Action. In: *Consciousness and Self-Regulation* (Davidson RJ, Schwartz GE, Shapiro D, eds), pp 1–18. Springer US. Available at: [http://link.springer.com/chapter/10.1007/978-1-4757-0629-1\\_1](http://link.springer.com/chapter/10.1007/978-1-4757-0629-1_1) [Accessed August 12, 2016].
- Norsworthy, A. N., & Visick, K. L. (2014). Gimme shelter: how *Vibrio fischeri* successfully navigates an animal's multiple environments. *Vibrio ecology, pathogenesis and evolution*, 142.
- Ogawa, T., & Komatsu, H. (2004). Target selection in area V4 during a multidimensional visual search task. *The Journal of Neuroscience*, 24(28), 6371-6382.
- O'Reilly, R. C., Herd, S. A., & Pauli, W. M. (2010). Computational models of cognitive control. *Current opinion in neurobiology*, 20(2), 257-261.
- Pais, D., Hogan, P.M., Schlegel, T., Franks, N.R., Leonard, N.E., & Marshall, J.A.R. (2013). A mechanism for value-sensitive decision-making. *PloS One*. 8:e73216
- Passino, K.M., Seeley, T.D., & Visscher, P.K. (2007). Swarm cognition in honey bees. *Behav Ecol Sociobiol* 62:401–414.
- Passingham, R. E., Stephan, K. E., & Kötter, R. (2002). The anatomical basis of functional localization in the cortex. *Nature Reviews Neuroscience*, 3(8), 606-616.

- Pasternak, T., & Greenlee, M. W. (2005). Working memory in primate sensory systems. *Nature Reviews Neuroscience*, 6(2), 97-107.
- Parvizi, J., Rangarajan, V., Shier, W.R., Desai, N., & Greicius, M.D. (2013). The will to persevere induced by electrical stimulation of the human cingulate gyrus. *Neuron*, 80:1359-1367.
- Paus, T. S. (2001). Primate anterior cingulate cortex: where motor control, drive and cognition interface. *Nature Reviews Neuroscience*, 2(6), 417-424.
- Pearson, J. P., Van Delden, C., & Iglewski, B. H. (1999). Active efflux and diffusion are involved in transport of *Pseudomonas aeruginosa* cell-to-cell signals. *Journal of bacteriology*, 181(4), 1203-1210.
- Pearson, J.M., Heilbronner, S.R., Barack, D.L., Hayden, B.Y., & Platt, M.L. (2011). Posterior cingulate cortex: adapting behavior to a changing world. *Trends Cogn Sci* 15:143–151.
- Pezzulo, G., Cisek, P. (2016). Navigating the Affordance Landscape: Feedback Control as a Process Model of Behavior and Cognition. *Trends Cogn Sci* 20:414–424.
- Picton, T. W., Stuss, D. T., Alexander, M. P., Shallice, T., Binns, M. A., & Gillingham, S. (2007). Effects of focal frontal lesions on response inhibition. *Cerebral Cortex*, 17(4), 826-838.
- Plaut, D.C. (1995). Double Dissociation without modularity: Evidence from connectionist neuropsychology. *Journal of Clinical and Experimental Neuropsychology*. 17:291-321.
- Posner, M.I., Snyder, & C.R.R. (1975). Facilitation and inhibition in the processing of signals. *Atten Perform V*:669–682.
- Postle, B. R. (2005). Delay-period activity in the prefrontal cortex: one function is sensory gating. *Journal of cognitive neuroscience*, 17(11), 1679-1690.
- Postle, B. R. (2006). Working memory as an emergent property of the mind and brain. *Neuroscience*, 139(1), 23-38.
- Postle, B. R. (2016). How Does the Brain Keep Information “in Mind”? *Current Directions in Psychological Science*, 25(3), 151-156.
- Porter, D. P., & Smith, V. L. (1994). Stock market bubbles in the laboratory. *Applied Mathematical Finance*, 1(2), 111-128.
- Pratt, S. C., Mallon, E. B., Sumpter, D. J., & Franks, N. R. (2002). Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis*. *Behavioral Ecology and Sociobiology*, 52(2), 117-127.
- Procyk, E., Tanaka, Y. L., & Joseph, J. P. (2000). Anterior cingulate activity during routine and non-routine sequential behaviors in macaques. *Nature neuroscience*, 3(5), 502-508.
- Reebs, S. G. (2000). Can a minority of informed leaders determine the foraging movements of a fish shoal?. *Animal behaviour*, 59(2), 403-409.

- Reynolds, C. W. (1987). Flocks, herds and schools: A distributed behavioral model. *ACM SIGGRAPH computer graphics*, 21(4), 25-34.
- Ridderinkhof, K.R., van den Wildenberg, W.P.M., Segalowitz, S.J., & Carter, C.S. (2004). Neurocognitive mechanisms of cognitive control: The role of prefrontal cortex in action selection, response inhibition, performance monitoring, and reward-based learning. *Brain Cogn* 56:129–140.
- Riley, M. R., & Constantinidis, C. (2015). Role of prefrontal persistent activity in working memory. *Frontiers in systems neuroscience*, 9.
- Roitman, J. D., & Shadlen, M. N. (2002). Response of neurons in the lateral intraparietal area during a combined visual discrimination reaction time task. *The Journal of neuroscience*, 22(21), 9475-9489.
- Robson, S. K., & Traniello, J. F. (1999). Key individuals and the organisation of labor in ants. In *Information processing in social insects* (pp. 239-259). Birkhäuser Basel.
- Rougier, N.P., Noelle, D.C., Braver, T.S., Cohen, J.D., & O'Reilly, R.C. (2005). Prefrontal cortex and flexible cognitive control: Rules without symbols. *PNAS*. 102:7338-7343.
- Rubia, K., Russell, T., Overmeyer, S., Brammer, M. J., Bullmore, E. T., Sharma, T., ... & Taylor, E. (2001). Mapping motor inhibition: conjunctive brain activations across different versions of go/no-go and stop tasks. *Neuroimage*, 13(2), 250-261.
- Rudebeck, P. H., Walton, M. E., Smyth, A. N., Bannerman, D. M., & Rushworth, M. F. (2006). Separate neural pathways process different decision costs. *Nature neuroscience*, 9(9), 1161-1168.
- Rumelhart, D.E., McClelland, J.L., Group, P.R., & others (1988) Parallel distributed processing. IEEE. Available at: <http://www.cs.toronto.edu/~fritz/absps/pdp2.pdf> [Accessed August 12, 2016].
- Rushworth, M. F., Noonan, M. P., Boorman, E. D., Walton, M. E., & Behrens, T. E. (2011). Frontal cortex and reward-guided learning and decision-making. *Neuron*, 70(6), 1054-1069.
- Ryle, G. (1949). Meaning and necessity. *philosophy*, 24(88), 69-76.
- Schall, J. D. (2001). Neural basis of deciding, choosing and acting. *Nature Reviews Neuroscience*, 2(1), 33-42.
- Schall, J. D., Stuphorn, V., & Brown, J. W. (2002). Monitoring and control of action by the frontal lobes. *Neuron*, 36(2), 309-322.
- Schoenbaum, G., Roesch, M.R., Stalnaker, T.A., Takahasi, Y.K. (2009). A new perspective on the role of the orbitofrontal cortex in adaptive behavior. *Nature Reveiws Neuroscience*. 10:885-863.
- Seeley, T. D. (2010). *Honeybee democracy*. Princeton University Press.
- Seeley, T. D., & Buhrman, S. C. (1999). Group decision making in swarms of honey bees. *Behavioral Ecology and Sociobiology*, 45(1), 19-31.

- Seo, H., & Lee, D. (2007). Temporal filtering of reward signals in the dorsal anterior cingulate cortex during a mixed-strategy game. *The Journal of Neuroscience*, 27(31), 8366-8377.
- Shallice, T. (1982). Specific impairments of planning. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 298(1089), 199-209.
- Sheth, S.A., Mian, M.K., Patel, S.R., Asaad, W.F., Williams, Z.M., Dougherty, D.D., Bush, G., & Eskandar, E.N. (2012). Human dorsal anterior cingulate cortex neurons mediate ongoing behavioural adaptation. *Nature*. 488:218-222
- Shenhav, A., Botvinick, M.M., & Cohen, J.D. (2013). The Expected Value of Control: An Integrative Theory of Anterior Cingulate Cortex Function. *Neuron* 79:217–240.
- Shenhav, A., Straccia, M. A., Botvinick, M. M., & Cohen, J. D. (2016). Dorsal anterior cingulate and ventromedial prefrontal cortex have inverse roles in both foraging and economic choice. *bioRxiv*, 046276.
- Shidara, M., & Richmond, B. J. (2002). Anterior cingulate: single neuronal signals related to degree of reward expectancy. *Science*, 296(5573), 1709-1711.
- Shiffrin, R.M., & Schneider, W. (1977). Controlled and automatic human information processing: II. Perceptual learning, automatic attending and a general theory. *Psychol Rev* 84:127–190.
- Shima, K., & Tanji, J. (1998). Role for cingulate motor area cells in voluntary movement selection based on reward. *Science*, 282(5392), 1335-1338.
- Simons, A. M. (2004). Many wrongs: the advantage of group navigation. *Trends in ecology & evolution*, 19(9), 453-455.
- Sleezer, B.J., & Hayden, B.Y. (2016). Differential Contributions of Ventral and Dorsal Striatum to Early and Late Phases of Cognitive Set Reconfiguration. *J Cogn Neurosci*:1–16.
- Sleezer, B.J., Cstagno, M.D., & Hayden, B.Y. (in Press). Rule encoding in orbitalfrontal cortex and striatum guides selection. *Journal of Neuroscience*.
- Smith, V. L., Suchanek, G. L., & Williams, A. W. (1988). Bubbles, crashes, and endogenous expectations in experimental spot asset markets. *Econometrica: Journal of the Econometric Society*, 1119-1151.
- Sporns, O., Tononi, G., & Kotter, R. (2005). The human connectome: a structural description of the human brain. *PLoS Computational Biology* 1:245-51.
- Sporns, O., & Betzel, R.F. (2016). Modular Brain Networks. *Annual Review of Psychology* 67:613:640.
- Stevens, A. M., Dolan, K. M., & Greenberg, E. P. (1994). Synergistic binding of the *Vibrio fischeri* LuxR transcriptional activator domain and RNA polymerase to the lux promoter region. *Proceedings of the National Academy of Sciences*, 91(26), 12619-12623.

- Stoll, F. M., Wilson, C. R., Faraut, M. C., Vezoli, J., Knoblauch, K., & Procyk, E. (2016). The effects of cognitive control and time on frontal beta oscillations. *Cerebral Cortex*, 26(4), 1715-1732.
- Strait, C.E., Blanchard, T.C., Hayden, B.Y. (2014). Reward Value Comparison via Mutual Inhibition in Ventromedial Prefrontal Cortex. *Neuron* 82:1357–1366.
- Strait, C. E., Sleszer, B. J., & Hayden, B. Y. (2015). Signatures of value comparison in ventral striatum neurons. *PLoS Biol*, 13(6), e1002173.
- Strait, C. E., Sleszer, B. J., Blanchard, T. C., Azab, H., Castagno, M. D., & Hayden, B. Y. (2016). Neuronal selectivity for spatial positions of offers and choices in five reward regions. *Journal of neurophysiology*, 115(3), 1098-1111.
- Strandburg-Peshkin, A., Farine, D. R., Couzin, I. D., & Crofoot, M. C. (2015). Shared decision-making drives collective movement in wild baboons. *Science*, 348(6241), 1358-1361.
- Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of experimental psychology*, 18(6), 643.
- Sumpter, D.J.T. (2006). The principles of collective animal behaviour. *Philos Trans R Soc Lond B Biol Sci* 361:5–22.
- Theraulaz G, Bonabeau E (1999) A Brief History of Stigmergy. *Artif Life* 5:97–116.
- Theraulaz, G., Bonabeau, E., & Deneubourg, J. L. (1998). The origin of nest complexity in social insects. *Complexity*, 3(6), 15-25.
- Treherne, J. E., & Foster, W. A. (1981). Group transmission of predator avoidance behaviour in a marine insect: the Trafalgar effect. *Animal Behaviour*, 29(3), 911-917.
- Turken, A.U., & Swick, D. (1999). Response selection in the human anterior cingulate cortex. *Nature Neuroscience*. 2:920-925
- Ursu, S., Stenger, V.A., Shear, M.K., Jones, M.R., & Carter, C.S. (2003). Overactive action monitoring in obsessive-compulsive disorder: evidence from functional magnetic resonance imaging. *Psychological Science*. 14: 347-354
- Van Veen, V., Krug, M. K., & Carter, C. S. (2008). The neural and computational basis of controlled speed-accuracy tradeoff during task performance. *Journal of Cognitive Neuroscience*, 20(11), 1952-1965.
- Visick, K. L., Foster, J., Doino, J., McFall-Ngai, M., & Ruby, E. G. (2000). *Vibrio fischeri lux* genes play an important role in colonization and development of the host light organ. *Journal of Bacteriology*, 182(16), 4578-4586.
- Volkow, N.D., Fowler, J.S. (2000). Addiction, a disease of compulsion and drive: involvement of the orbitofrontal cortex. *Cerebral Cortex*. 10:318-325.
- Wallraff, H.G. (1978). Social interrelations involved in migratory orientation of birds: possible contributio of field studies. *Oikos* 30:401-404.
- Wang, X. J., & Kennedy, H. (2016). Brain structure and dynamics across scales: in search of rules. *Current opinion in neurobiology*, 37, 92-98.

- Wang, Z., Dai, Z., Gong, G., Zhou, C., & He, Y. (2015) Understanding structural-functional relationships in the human brain: A large-scale network perspective. *The Neuroscientist* 21:290-305.
- Ward, A.J.W., Sumpter, D.J.T., Couzin, I.D., Hart, P.J.B., & Krause, J. (2008). Quorum decision-making facilitates information transfer in fish shoals. *Proc Natl Acad Sci* 105:6948–6953.
- Waters, C. M., & Bassler, B. L. (2005). Quorum sensing: cell-to-cell communication in bacteria. *Annu. Rev. Cell Dev. Biol.*, 21, 319-346.
- Weiner, N., & others (1948). *Cybernetics*. New York: Wiley.
- Wilson, E. O. (1971). The insect societies. *The insect societies*.
- Wilson, R.C., Takahashi, Y.K., Schoenbaum, G., & Niv, Y. (2014). Orbitofrontal Cortex as a Cognitive Map of Task Space. *Neuron* 81:267–279.
- Wilson, C. R., Gaffan, D., Browning, P. G., & Baxter, M. G. (2010). Functional localization within the prefrontal cortex: missing the forest for the trees?. *Trends in neurosciences*, 33(12), 533-540.
- Wickelgren, W. A. (1977). Speed-accuracy tradeoff and information processing dynamics. *Acta psychologica*, 41(1), 67-85.
- Zhu, J., & Winans, S. C. (1999). Autoinducer binding by the quorum-sensing regulator TraR increases affinity for target promoters in vitro and decreases TraR turnover rates in whole cells. *Proceedings of the National Academy of Sciences*, 96(9), 4832-4837.