

Control without controllers: Towards a distributed neuroscience of executive control

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1 **Abstract**

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3 Executive control refers to the regulation of cognition and behavior by mental
4 processes and is a hallmark of higher cognition. Most approaches to understanding its
5 mechanisms begin with the assumption that our brains have anatomically segregated and
6 functionally specialized control modules. The modular approach is intuitive: control is
7 conceptually distinct from basic mental processing, so an organization that reifies that
8 distinction makes sense. An alternative approach sees executive control as self-
9 organizing principles of a distributed organization. In distributed systems, control and
10 controlled processes are co-localized within large numbers of dispersed computational
11 agents. Control then is often an emergent consequence of simple rules governing the
12 interaction between agents. Because these systems are unfamiliar and unintuitive, here
13 we review several well-understood examples of distributed control systems, group living
14 insects and social animals, and emphasize their parallels with neural systems. We then re-
15 examine the cognitive neuroscience literature on executive control for evidence that its
16 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?

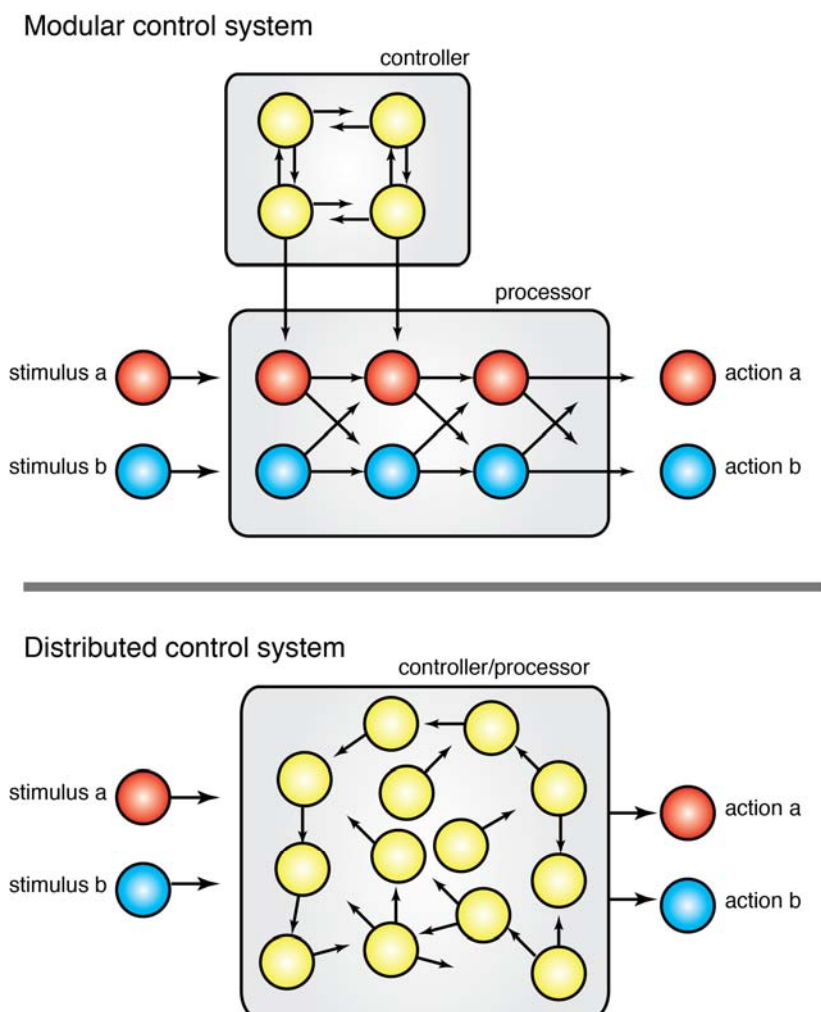
Modular and distributed control systems

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).

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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 (GOFAI)-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.

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117 **II. Principles of distributed control systems**

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119 **Principle 1: Horizontal information flow**

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

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

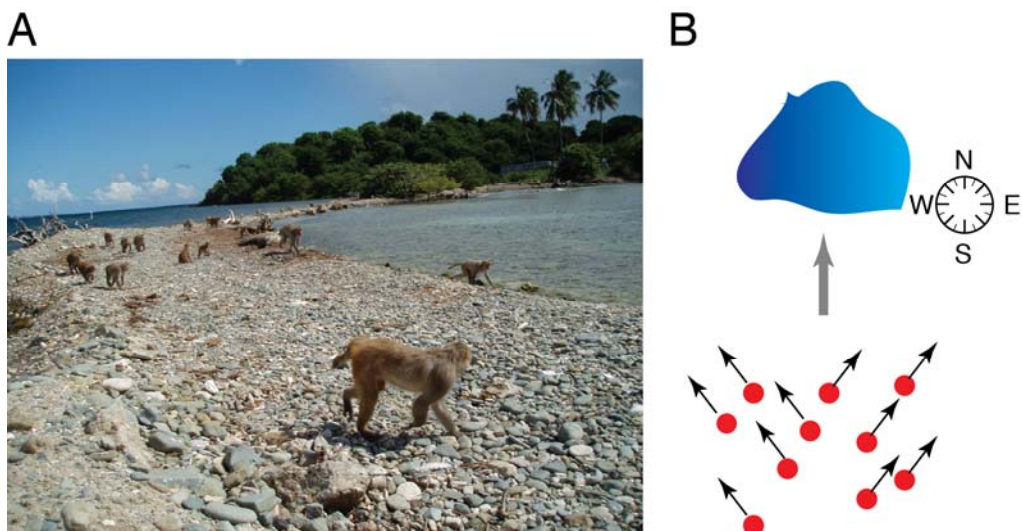
132 Simpson, 2007; Simons, 2004; Hamilton, 1967; Bergman & Donner, 1964; Walraff,
133 1978; Mallon, Pratt, & Franks, 2001; Conradt & Roper 2003). The baboon troop thus
134 uses a collective decision-making strategy. Individuals begin to head off towards their
135 best guess and as they do this, troop 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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168 **Figure 2.** Group movement strategies often illustrate the principle of horizontal
169 information transfer. **A.** Rhesus monkey troops on Cayo Santiago migrate multiple times
170 each day and may use distributed consensus procedures to choose a direction. **B.**
171 Cartoon birds eye view illustrating split voting situation. If the troop is split between a
172 northeast and a northwest direction, the consensus will not be the average (north) but
173 one of the two modal directions.

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).
196

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).
221

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.

249

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).



260
261 **Figure 4.** Simple rules of distance and spacing determine the shapes of both fish
262 schools and bird flocks. [Fish picture: Gordon Firestein - Seacology USA, Bird Flock:
263 Faisal Akram]
264

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

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

283 Presumably, we can classify control systems on a spectrum from fully distributed
284 and leaderless to strictly segregated and hierarchical; the specific organization observed
285 for any system will depend on the environment in which it evolved. This fact is important
286 to remember when considering neural systems, which may have some specialization of
287 function (Botvinick et al., 2001; Rougier et al., 2005; Kanwisher, Mcdermott, & Chun,
288 1997).

289 **Principle 5: Quorum-sensing**

290 Agents in distributed systems have very limited field of view in their monitoring
291 capabilities. In other words, it is often difficult to see the forest for the trees. But
292 sometimes it is critical to see the forest to make the best decision. In these cases, agents
293 must engage in *quorum-sensing*: a type of consensus-based control mechanism wherein a
294 set threshold or quorum determines the course of action (Mitchell, 2009).
295

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.

319

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

321

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.

336

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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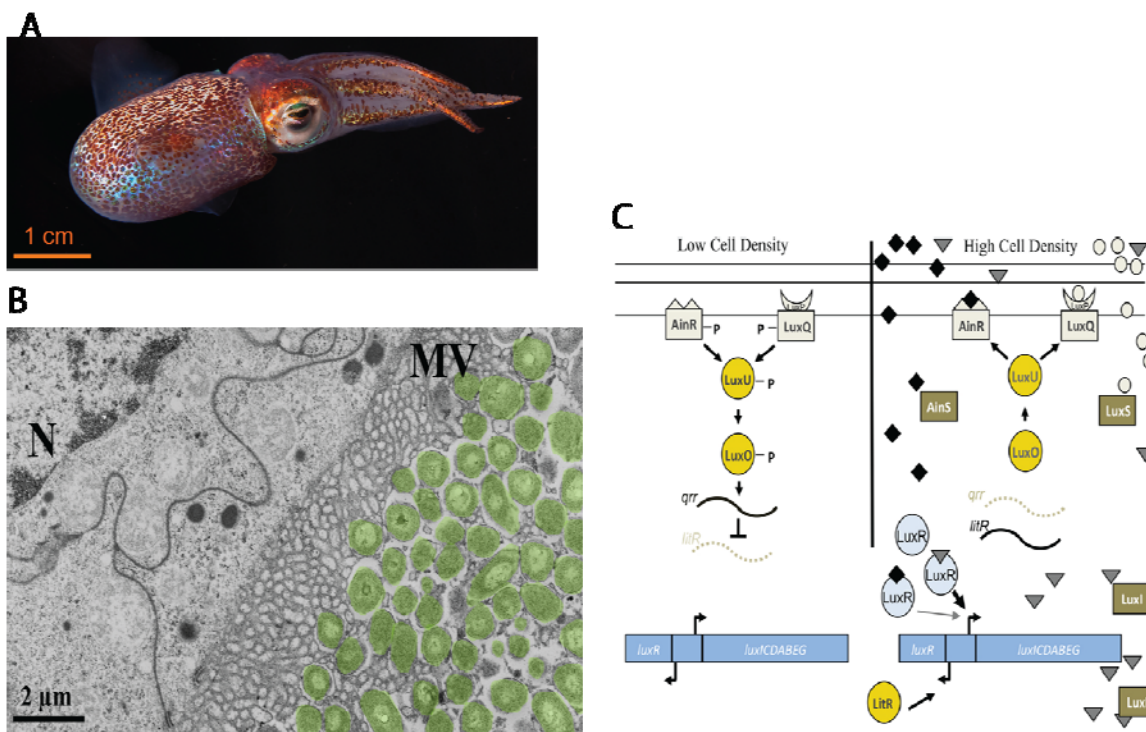


Figure 5. **A.** Hawaiian squid (*Euprymna scolopes*). **B.** Image of *V. fischeri* embedding into microvilli of host epithelial cells. **C.** Illustration of control circuit for regulation of luminescence through chemical detection in *V. fischeri*. Credits: (A,B) reproduced with permission from “Divining 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).

400

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.

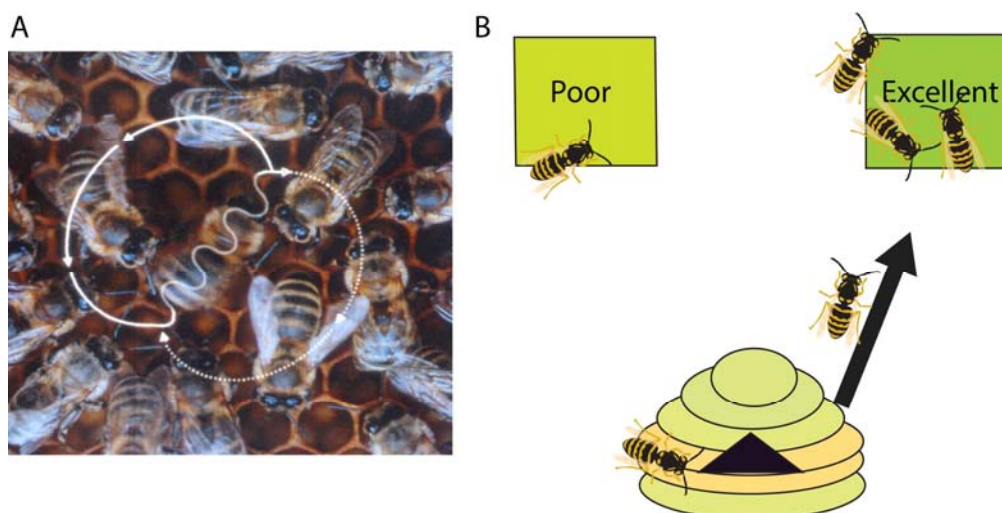
450

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

506

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., 19999; 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 (Hokosawa 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” (Misisic & 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).
791

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