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## The Evolutionary Origins of Cognitive Control

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### Abstract

The question of domain-specific versus domain-general processing is an ongoing source of inquiry surrounding cognitive control. Using a comparative evolutionary approach, Stout (2010) proposed two components of cognitive control: coordinating hierarchical action plans and social cognition. This article reports additional molecular and experimental evidence supporting a domain-general attentional process coordinating hierarchical action plans, with the earliest such control processing originating in the capacity of dynamic foraging behaviors—predating the vertebrate-invertebrate divergence (c. 700 million years ago). Further discussion addresses evidence required for additional, domain-specific, cognitive control processes, noting that proposed social processes may simply provide emotionally valenced representational information to the above hierarchical process.

*Keywords:* Evolutionary psychology; Comparative biology; Executive control; Foraging; Dopamine; Social evolution

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### 1. Introduction

Cognitive control has at times been regarded as having the domain-generality of a Turing machine (Samuels, 2008) or the domain-specificity of a Swiss army knife (Cosmides & Tooby, 1994). Such positions are closely related to stances taken by many models of cognitive architecture, in which an executive process is considered to be either a domain-general component of the cognitive system or an emergent property of competing subsystems (see Miyake & Shah, 1999). In a recent issue of this journal devoted to understanding the componential or emergent aspects of cognitive control, Stout (2010) used a comparative evolutionary approach to argue for the existence of two domains of cognitive control: One for the regulation of hierarchically structured action sequences and one for social cognition.

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Here, I provide additional evidence for a control process devoted to hierarchically structured action, pointing out how the neural correlates of such control are shared across vertebrates and invertebrates alike—in ways that predictably modulate persistence on action plans. I argue that such processes appear to have evolved in the control of dynamic foraging and feeding related behaviors prior to the invertebrate-vertebrate divergence. I also provide evidence that Stout's (2010) proposed social control process adds nothing to the more general hierarchical process outlined above, beyond providing domain-specific information available in social representations. While I focus the points I make here on Stout's (2010) article, the issues I address apply more generally to the componential-versus-emergent question of cognitive control (e.g., Cooper, 2010; Lenartowicz, Kalar, Congdon, & Poldrack, 2010).

## **2. The evolutionary origins of a domain-general cognitive control process**

Miller, Galanter, and Pribram's (1960) initial description of "working memory" was in terms of a "memory we use for the execution of our Plans" (p. 65), where "a Plan is any hierarchical process in the organism that can control the order in which a sequence of operations is to be performed" (p. 16). Hierarchically structured actions have been employed by numerous models of cognition, such as the General Problem Solver (Newell & Simon, 1972), ACT-R (Anderson et al., 2004), and SOAR (Laird, Newell, & Rosenbloom, 1987). Moreover, numerous tasks can be represented as subgoal hierarchies and this has become an increasingly plausible conceptualization of executive control processes (e.g., Botvinick, 2008; Braver & Bongiolatti, 2002).

Stout (2010; also see Byrne & Russon, 1998; Byrne, 1997) proposes that the faculty for implementing hierarchically structured action sequences evolved partly in response to foraging among our hominid ancestors. While this may be so, the neuromolecular and behavioral evidence from across animal (i.e., metazoan) species points to an origin for the components of cognitive control prior to the invertebrate-vertebrate divergence (approximately 700 million years ago; see Ayala, Rzhetsky, & Ayala, 1998). They also point to a specific functional mechanism that is a keystone in flexible cognitive control.

As Stout (2010) notes, many other animal species besides humans exhibit control processing that appears to be related to flexible intelligence (Emery & Clayton, 2004; Marino, 2002). More or less flexibility is frequently associated with being able to appropriately mediate persistence in action: Giving up on a failing course of action or persisting when actions are successful. In spatial foraging behavior, this flexibility is associated with appropriately shifting foraging strategies between local exploitation and global exploration, a behavioral characteristic found in a wide variety of species, including ants, nematodes, flies, and humans (e.g., Bell, 1991; Hills, Brockie, & Maricq, 2004; Kalff, Hills, & Wiener, 2010; Wehner & Srinivasan, 1981).

Across many species, conserved neuromolecular processes associated with dopamine underlie locomotory flexibility (e.g., Bainton et al., 2000; Ralph, Paulus, Fumagalli, Caron, & Geyer, 2001). Dopaminergic (DA) neuromodulatory microcircuits similar to those found modulating locomotory control in other species (e.g., in nematodes, Hills et al., 2004) are

also found throughout the vertebrate striatum (Dani & Zhou, 2004). This is a region associated with executive processing, attentional control, and its connections to the prefrontal cortex. In most all cases, downstream neural activation is mediated by the DA modulation of G-protein linked receptors, which induce a cascade of intracellular events that modulate cellular responses to other neurotransmitters—commonly, glutamate (see Konradi & Heckers, 2003). Though DA receptors are both excitatory and inhibitory, together the receptors are argued to enhance the signal-to-noise ratio of a given neural message, facilitating activity locally while inhibiting activity more globally (Seamans, Gorelova, Durstewitz, & Yang, 2001). In other words, this mediates persistence in neural activation. In invertebrates, enhanced DA activity is often found to be associated with persistence in action regarding local spatial exploitation and feeding behavior (e.g., Bainton et al., 2000; Hills et al., 2004). In vertebrates, enhanced DA activity is associated with stereotypic behavior (e.g., Posey & McDougle, 2000) and cognitive perseveration (e.g., Boulougouris, Castane, & Robbins, 2009).

The ubiquity of this relationship between molecular mechanisms and behavior across species begins to resolve an evolutionary hypothesis for the origins of cognitive control, with the control of goal-directed cognition following as an evolutionary descendent of animal foraging behavior (proposed in Hills, 2006). This further suggests that spatial search and goal-directed behavior are evolutionarily *homologous*, derived from the same function: mediating persistence in action.

Recently, we investigated whether cognitive control, and its capacity for mediating persistence in action, might be a component of a general cognitive architecture that facilitates search both in space and in more general hierarchical goal-directed behavior. This involved priming search behavior between two putative slave systems of working memory—from an external visuospatial search task to an internal lexical search task (Hills, Todd, & Goldstone, 2008; Hills, Todd, & Goldstone, 2010). Participants first searched for resource pixels on a two-dimensional array displayed on a computer screen, and then moved to a word search task involving finding multiple words among groups of random letters (e.g., BLNTAO). Participants who first foraged in a clustered spatial environment (vs. a diffuse spatial environment) subsequently searched as if there were more (or fewer) words among a group of letters in the word search task. The priming also influenced search at multiple hierarchical levels within the lexical task (e.g., similarity between sequential solutions). We tested and found support for a model that explained these results in terms of an executive mediation of subgoal persistence: Priming perseveration on subgoals in the spatial environment enhances perseveration on hierarchically arranged subgoals in subsequent environments.

In summary, neural, comparative, and recent priming studies support a domain-general cognitive control process in humans that mediates subgoal persistence in hierarchically structured action sequences—with the neural precursors of cognitive control originating in the capacity of spatial foraging prior to the invertebrate-vertebrate divergence. Importantly, this domain-general aspect of cognition aids in addressing the componential-versus-emergent properties of cognitive control (see Cooper, 2010) by providing baseline criteria for additional components of cognitive control.

### 3. Criteria for novel cognitive control processes: The question of social processing

When proposing a novel component of cognitive control, there are two questions that must be addressed: First, is the component process a control process, or *is it a representational process* that channels domain-specific information to other control processes (Samuels, 2008)? Second, is the component process domain-specific, or *is it simply one of the many potential capacities of other, potentially more general control processes* (this thorny issue is discussed in detail by Atkinson & Wheeler, 2004)? These questions should be asked of any proposed domain-specific control processes (e.g., social contract algorithms, see Cosmides, 1989).

Stout's (2010) argument for a social control process is based on three observations related to the ventromedial prefrontal cortex (VMPFC): (a) evidence that damage to this area influences social processing, (b) correlations between the size of portions of this area and social group size across primate species, and (c) the observation that this area is associated with the capacity to facilitate the abilities required for adaptive social behavior. However, based on the above questions, social cognition, nonetheless, fails to meet the criteria of a separate componential control process.

As noted by Stout (2010), the VMPFC is not specific to social functions; it is also involved in the somatic marker hypothesis—proposed as a mechanism for integrating emotional information in the control of decision making (Damasio, 1994). This would explain the VMPFC's involvement in tasks associated with emotion-inducing consequences, like monetary losses and gains, such as the Iowa Gambling Task (Bechara, Damasio, Damasio, & Anderson, 1994). Moreover, if the VMPFC houses components for integrating emotional information, this predicts its involvement in a wide range of behaviors (including social behaviors) involving retrieval of information from emotional representations. Rather than a social control process, the VMPFC may be better conceptualized as an affective process used to weight potential courses of action using information acquired from memory representations.

Processes associated with *theory of mind* (ToM) also do not support a social control process. In a review of ToM, Gallagher and Frith (2003) argue that the anterior paracingulate, a portion of the VMPFC, is associated with ToM processing. They cite evidence showing that when participants played a “game of rock, paper, scissors,” the anterior paracingulate was active if the participants thought they were playing against a person, but not active when they believed they were playing against a computer. Activity in the anterior paracingulate was the main effect of the contrast between these two conditions. However, the anterior paracingulate is also active when people see pictures of familiar persons (Liebenluft, Gobbini, Harrison, & Haxby, 2004). Again, this is consistent with the notion that ToM (and other social processing) is mediated strongly by the capacity to *recall* what other people would do, and weight potential actions accordingly. Leslie, Friedmann, and German (2004) provide a similar account of ToM as a domain-general attentional selection process, which is biased by domain-specific representational information.

The executive demands of social life proposed by Byrne and Bates (2007; cited in Stout, 2010) support the argument that social processing is but one capacity of a more general

control process: Simply replacing the word “individuals” with “objects” and removing the word “social,” their list of abilities required for (social) cognition are “a) recognizing different [objects] and signals, b) focusing sustained attention on relevant...stimuli, and c) rapid learning of associations.” All of these would be beneficial for learning when and where to forage, predicting the presence or absence of predators, and most any other reasoning and decision-making tasks associated with implementing hierarchical action plans. In sum, the argument is that domain-general hierarchical control processing can use social information like it uses spatial information, or memory for mathematical facts. It is not clear that anything else unique to social control processing is taking place.

At some point, the prerequisites for a social or other domain-specific control process may come to light—that is, evidence that they are not the result of accessing domain-specific representations and that they offer something unique to control not facilitated by more general processes. For social control, we are perhaps better served by a model of domain-specific representation proposed by Jackendoff (1992)—one based on a universal grammar of innate social representations. Similar representational access may account for numerous apparently domain-specific control behaviors, such as language acquisition and mate selection. Similar to the way the specific blades of a Swiss army knife are controlled by an all-purpose handle, the activation of domain-specific, algorithmic representations could be mediated by the domain-general hierarchical control processes proposed above—for which we already have strong cognitive, neuromolecular, and comparative evolutionary evidence.

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