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Cognitive Science: Persistent Apes Are Intelligent Apes

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In humans, self-control is correlated with general intelligence; a new study finds that this correlation extends to chimpanzees as well. The new results highlight the cognitive bases of self-control and suggest a common evolutionary history for human and primate self-control.

Self-control is among the most difficult of cognitive processes to understand, and also to study [1]. Most of us have a strong intuition about what self-control is, but it is nonetheless difficult to define rigorously enough to study in the laboratory. The field is characterized not only by the standard empirical debates, but also by elementary definitional debates about what is and is not self-control, and whether it is a single thing or multiple distinct things [2,3]. These issues, difficult enough to approach in human studies, loom even larger in animal studies, where we cannot directly talk to our subjects [4,5]. A new study by Beran and Hopkins, reported in this issue of *Current Biology* [6], makes a great stride by linking self-control to general intelligence in chimpanzees.

Despite the difficulty in defining and measuring self-control, the problem is not merely philosophical. Indeed, understanding self-control is vitally important. Diminished self-control is a defining feature of many diseases, including addiction and depression, and treatments designed to improve self-control ameliorate these problems [7]. Self-control is also a central player in a wider variety of social problems, including obesity and educational disparities. As in psychiatric diseases, treatments designed to improve self-control have shown some preliminary successes (for example [8]).

These possible links between self-control and other aspects of cognition suggest that a fertile path for studying self-control is to focus on the broader links between measures of self-control and more general measures of cognitive functioning. General intelligence is linked to many important features of the mind, and as such provides a valuable entry point into much of cognition. In humans, general intelligence has been linked with the ability to delay immediate gratification in favor of larger future gain, a trait that is closely related to self-control [9]. Likewise, children's performance in the classic marshmallow task, which involves persisting in a decision to refrain from eating a single marshmallow, has been linked with scores on general intelligence tests [10]. These links suggest that a common set of mental functions may underlie a wide variety of cognitive abilities.

The field of animal self-control is beset by a dearth of validated measures. For example, the inter-temporal choice task is perhaps the most widely used tool for studying self-control in nonhuman animals; however, foraging-inspired critics have argued that the test measures task understanding and attentional bias, psychological factors that are important, but that are not strictly self-control [11,12]. Nonetheless, understanding self-control in animals is extremely important: it is much easier for scientists to measure and manipulate brains in nonhuman animals than in humans. Moreover, studying a variety of animal species gives us a broader picture: by comparing across species, we can understand the general properties of self-control and its evolution [13].

In their new study, Beran and Hopkins [6] show that self-control in apes is associated with general intelligence. They took advantage of two heretofore unrelated, but felicitous, methodological advances. First, Hopkins and colleagues have developed a robust measure of ape intelligence; these measures are focused on the domains of physical social cognition, not elements that have any clear connection to inhibitory processing. Second, Beran and colleagues [14,15] have developed original techniques for measuring self-control in animals; this work bypasses problems with previous measures of self-control.

Unlike typical inter-temporal tasks, animals performing the Hybrid Delay Task have the option of ending the delivery of the large reward early by taking the accrued food items before the entire reward set has been delivered. This means that aspects of maintenance during the delay period can be dissociated from choice artifacts dealing with preferences for larger rewards. Indeed the drive to impulsively point to larger rewards is a confound for many types of inter-temporal choice tasks [16]. By allowing for early termination of reward accrual a critical element of self-control, persistence within a selected behavior pattern, can be directly measured.

Importantly, the strongest intelligence correlate with self-control that Beran and Hopkins [6] observed is a component that they call efficiency, which measures persistence, not self-controlled choice. This result is consistent with the idea that the ability to persist across time in the face of temptation is the key to self-control; in comparison, the ability to choose the controlled option tends to be weakly correlated, if at all, with self-control in both humans and animals. This idea is reminiscent of the observation that behavior in the Marshmallow task (a persistence task) is strongly predictive of later measures of success, but behavior in the inter-temporal choice task (which does not require persistence) is only modestly correlated. These results then provide some validation for the idea that the intertemporal choice task is a poor measure of self-control in animals, and that using tasks that require persistence in animals will be critical for an understanding of self-control [17,18].

That self-control performance and general intelligence share a relationship in both humans and primates raises interesting possibilities for gaining further insights into the evolution of intelligent behavior. It may be that selective pressures for inhibitory processes may have served as a driver for primate cognitive evolution. Such an explanation would account for the relationship between the ability of primates to withhold responding in order to gain larger rewards and intelligence. Alternatively it may be that cognitive monitoring may underlie successful performance in both the hybrid delay task and tests of general intelligence. Evidence that monitoring, a metacognitive process, is the key link, comes from the strong observed relationship between efficiency (which requires monitoring) with general intelligence but not preferences for larger later options (which does not).

These results are still somewhat speculative — as they should be given the innovation demonstrated here. One interesting debate in the recent literature is whether self-control is somehow qualitatively different from other forms of economic choice [19,20]. If there is no important difference, then self-control may relate to general intelligence because it is just one way of asking about the coherent functioning of the brain systems involved in integrating information about the environment to guide adaptive behavior.

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Evolution: Vertebrate Limb Control over 420 Million Years

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The neural circuits that control elasmobranch fins and the mammalian limbs have been found to exhibit striking similarities at the molecular, cellular and behavioral levels. The implication is that the neural substrate underlying limb control had already evolved 420 million years ago.

From lamprey to the sting ray and primates, the locomotor system is organised in a generally similar way, with a midbrain locomotor command region (MLR) that activates spinal circuits responsible for generating the motor pattern, whether undulatory swimming in fish or walking movements in limbed vertebrates [1,2]. The trunk movements are generated by activation of segmental motoneurons in the medial motor columns (MMC), whereas the flexor and extensor motoneurons of the limbs in mammals are located in a separate lateral motor column (LMC). The oldest group of vertebrates with appendages (fins or legs) is the elasmobranchs (sharks and rays) which have had a separate evolutionary history from that of mammals for over 420 million years (Figure 1). This group of animals, specifically the skate *Leucoraja erinacea*, is the focus of a new and evolutionarily important study by Jung *et al.* [3], who combined genetics with behavioral and anatomical analyses to show that the molecular networks identified in mammals also operate in the phylogenetically much older group of elasmobranchs.

Elasmobranchs such as skates and rays swim by transmitting undulatory

waves along their extended pectoral fins. When moving on the bottom of the sea, however, they can instead use their pelvic fins to generate what looks like walking with alternating movements using their limb-like appendages. Both the pectoral and pelvic fins are divided into two opposing muscle compartments, akin to the flexors and extensors of the mammalian limbs. These muscles are innervated by motoneurons located in a separate motor column (*le*LMC, *Leucoraja* LMC) similar to the mammalian LMC. Within the *le*LMC, 'flexor' and 'extensor' motoneurons are spatially segregated: they extend their axons to the ventral roots, where they subsequently divide into a dorsal and ventral nerve branch supplying the dorsal and ventral muscle mass, respectively, in a similar way to the innervation of the mammalian limb. The motoneurons innervating the trunk are located in a separate MMC that is present in all segments along the body.

The *le*LMC motoneurons express the gene *Foxp1*, which disinguishes mammalian LMC neurons, which express the marker, and MMC neurons, which do not. The *le*LMC also expresses

the genes for the transcription factors required to specify core features of mammalian motoneuron identity: *Hb9*, *Isl1/2* and *Lhx3* genes. Similarly, motoneurons expressing *Lhx1* project to the dorsal muscle mass dependent on induction of EphA4, while those innervating the ventral muscle mass express *Isl1* and their axons take a ventral course specified by expression of *EphB1*, as in mammals. Jung *et al.* [3] also show that *Foxp1* neurons of the LMC are present in a variety of sharks as well as in teleosts, such as zebrafish, testifying to the generality of the conclusions that the origin of the LMC innervation of appendages, as studied in mammals, dates back to early vertebrate history 420 million years ago, when the elasmobranchs diverged from the vertebrate line leading up to mammals.

With regard to the *Hox* genes expressed in the pectoral and pelvic regions, the profiles are analogous to those in forelimb and hindlimb LMC motoneurons of mammals [4,5]. The expression of *Hox9* analogs leads to a suppression of *Foxp1* and the entire LMC in both the skate and in mammals [3]. This occurs for instance in the thoracic