

~2.3 to 1.8 billion years ago display relatively large ratios compared to either older or younger pyrites. This breakdown of Earth history is particularly interesting because it coincides with current views of the redox evolution of the biosphere: Stage 1 (more than ~2.3 billion years ago), in which the atmosphere and much of the ocean were free of oxygen; Stage 2 (from ~2.3 to ~1.8 billion years ago), when the atmosphere became oxidized but the ocean remained anoxic and perhaps mildly sulfidic; Stage 3a, characterized by deep-ocean euxinia (from ~1.8 to ~0.75 billion years ago); and Stage 3b (from ~0.75 billion years ago to the present), during which, with the exception of brief "oceanic anoxic events" (7), both the ocean and atmosphere were oxygenated (8, 9). During Stage 1, the oceans became enriched in iron during periods of submarine volcanism. At the same time, iron was being removed from the ocean as both iron oxides [including the voluminous banded iron formations (BIFs) upon which much of the world's steel production depends] and pyrite. Iron oxides were formed in the water column either by anaerobic oxidation or by small amounts of oxygen that accumulated in regions of the surface ocean with high cyanobacterial productivity. BIF was

demonstrably enriched in ^{56}Fe ; its deposition drove the ocean toward lower values of $\delta^{56}\text{Fe}$, as recorded in the pyrites (see the figure). Stage 2 witnessed a waning of volcanism and associated BIF, and thus a shift toward a dominance of the pyrite-removal mechanism for iron and higher oceanic values of $\delta^{56}\text{Fe}$. Renewed BIF at 1.8 billion years ago lowered the marine iron isotope ratio at the beginning of stage 3a. Subsequent sulfidic (8, 9) or oxygenated (10) conditions in the deep sea ensured that aqueous iron did not accumulate in the ocean but rather was removed as an insoluble component of the sediment, thus retaining the isotopic composition of the Fe inputs to the ocean at very close to the crustal average ($\delta^{56}\text{Fe} \approx 0\%$).

As is always the case during the early development of paleoenvironmental proxies, more observations are needed before firm, globally relevant interpretations can be made. If the trends do persist, though, a number of outstanding questions may eventually be answered: Was iron an important component of the Precambrian oxygen balance? Was BIF deposition a major sink for iron throughout the Precambrian before 2.3 billion years ago, or was its deposition more episodic, separated by long intervals of non-BIF deposition (11)? Was the end of BIF deposition the result

of the establishment of oxygenated (10) or sulfidic (8, 9) deep-ocean conditions? Did Phanerozoic (since 542 million years ago) oceanic anoxic events leave tell-tale iron-isotope signatures? Ultimately, we will be able to use the iron isotopes, as we've used carbon and sulfur isotopes, to put quantitative constraints on rates of Precambrian iron cycling, and thus on the extent to which iron provided a source or sink for oxygen during this critical interval of Earth history.

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9. The stage designations are those of (2), except that Stage 3 is divided into euxinic (3a) and oxygenated (3b) substages. According to (10), there was no stage 3a (interval of oceanic euxinia); the oceans became oxygenated at 1.8 billion years ago.
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NEUROSCIENCE

Adaptive Coding

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A century ago, psychologists considered cognitive control to be a major player in decision-making (1, 2). Yet, the study of how perception and action are mediated by instructions and intentions entered a twilight zone during the middle part of last century as behaviorists turned their backs on mental processes that they could not directly observe. It was not until the turn of the millennium that psychologists and neuroscientists regained their interest in understanding how the human brain regulates the flow of information to achieve intended goals. Notably, this resurgence of interest in cognitive control (3) coincided with methodological innovations such as functional magnetic resonance imaging (fMRI) and electrical recordings from single neurons. Such techniques enable dissection of the brain activities that

underlie mental operations. Two studies, on pages 1121 (4) and 1118 (5) of this issue, nicely illustrate another development that may boost investigation of cognitive control beyond its renaissance. The new work was inspired by the notion that neurons in the frontal region of the brain (or neuronal ensembles, or even brain areas) may dynamically and adaptively switch between multiple functions rather than statically accomplishing preset tasks.

In their study, Machens and colleagues (4) inserted tiny electrodes into the prefrontal cortex of monkey brains to record the firing rates of single neurons while the monkeys performed a dynamic decision-making task. The task involved the comparison of two quantities (two frequencies of vibration presented to a fingertip), separated by a brief delay. The mental operations involved in this quantity-comparison task included (i) perceiving the first signal (S1), (ii) holding it in working memory for several seconds, and (iii) perceiving the second signal (S2) and deciding whether it was of lower or higher quantity than the first.

Some monkey neurons expressed a clear

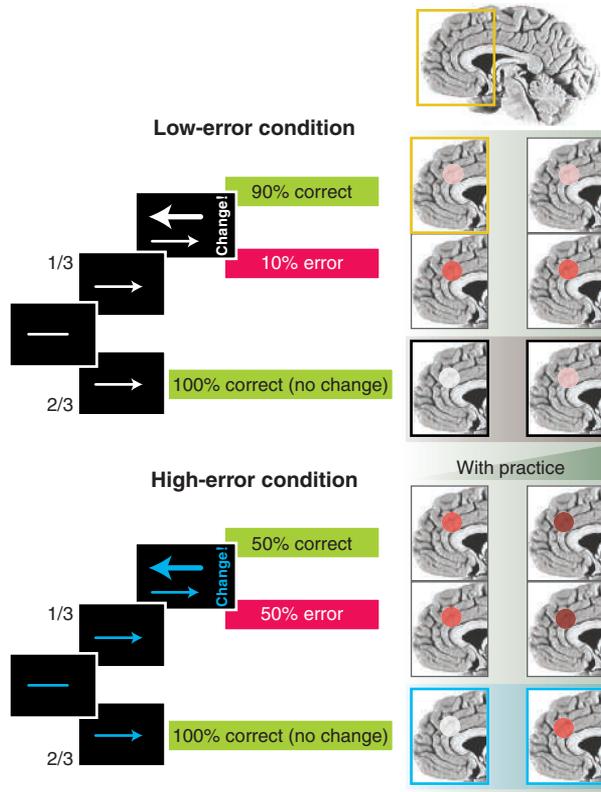
preference for the low vibration frequency (quantity), whereas others fired preferentially in response to the higher quantity. Although neurons in the secondary somatosensory cortex of monkey brain remained silent in the delay interval between S1 and S2, their preferences for the low versus the high quantity remained invariant. Neurons in the prefrontal cortex, by contrast, showed differential preferences for the low versus the high quantity not only during the presentation of S1, but throughout the delay interval, during which they sustained their preferential firing patterns. In the decision phase, however, prefrontal cortex neurons no longer encoded information about high versus low quantities, but rather encoded information for "S2 < S1" or "S2 > S1", respectively. Thus, the firing rates of single neurons in the prefrontal cortex first encode the quantity of S1, then represent the active maintenance of that quantity in working memory, and finally reverse sign to encode the appropriate decision. Computer simulations of firing in a neural network, which capitalize on mutual inhibition between opposing units, confirmed the firing patterns produced by real neurons as observed by Machens and co-workers. Their study provides a fruitful synthesis of real-world neurophysiological data with the nonlinear modeling of dynamic systems. The Machens *et al.* results clearly show that networks of prefrontal cortex neurons

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can dynamically adapt and reconfigure the encoding functions represented in their firing patterns as the cognitive flow develops, without changing their connectivity.

Nevertheless, the question remains: How do neurons “know” when to encode a particular activity? A larger scale implementation of adaptive coding, like that introduced by Brown and Braver (5) in their new study, may provide some answers. Cognitive control should not simply be considered a basic mental function supported by static, dedicated neural systems. Instead, instantiations of cognitive control should be envisioned as emergent properties of the neural network configuration, with more elementary mechanistic processes being tailored to allow new and unique functions to emerge (3). The notion of “adaptive coding” applies not only to within-trial changes in the firing patterns of prefrontal cortex neurons, but also to the emergence of cognitive control through learning. For example, the specialized higher order nature of a process called performance-error monitoring may be a new function that emerges from more basic neural mechanisms for conflict detection. Such conflict-detection mechanisms usually reside in medial frontal cortex (MFC) neurons, which detect the simultaneous activation of competing correct and incorrect responses (6). Brown and Braver (5) take this notion one step further with their proposal that both error detection and conflict monitoring are special cases of a more fundamental computational process in which activation of MFC neurons is proportional to the perceived likelihood of an error taking place.

Brown and Braver assume that representations of the likelihood of error by the MFC develop through experience. Such representations build on reinforcement-learning processes that are mediated by phasic decreases in midbrain dopamine projections to the MFC when ongoing events turn out worse than expected (7, 8). To test their assumption, the investigators invited human volunteers to perform a stop-change task (9) in which a rapid left- or right-hand button-press response is designated by the direction of an arrow (see the figure). This response requires reversing in one-third of the trials when a second arrow pointing in the opposite direction is presented at a later time point. The second arrow is presented at variable time intervals after the first, calibrated so as to produce error rates of 10% or 50% unchanged



Predicting error likelihood. In Brown and Braver’s fMRI study, human volunteers undertook a stop-change task. In this task, a rapid left- or right-hand button-press response is designated by the direction of an arrow; this response must be reversed when a second arrow pointing in the opposite direction is presented (5). The task uses a tracking algorithm that adjusts the time of presentation of the change-signal (opposite arrow) and hence controls the likelihood of making an error. On each trial, the error likelihood is indicated in advance by a color cue (blue for high error, white for low error). With blue-color cues, human volunteers had a harder time changing their response after a change signal (50% errors) than with white-color cues (10%). Brain areas highlighted in red indicate MFC regions that are activated by the stop-change task (the greater the MFC activation, the deeper the red color). Most importantly, during no-change trials (which lack error-inducing tactics and thus lack conflict), MFC activity increased with practice, especially in response to blue color cues, reflecting an improved ability to predict the likelihood of making an error.

responses (low-error and high-error conditions, respectively). On each trial, the error likelihood is indicated in advance by a color cue (blue for high-error likelihood, white for low-error likelihood). During execution of the stop-change task, fMRI revealed greater activity in the MFC during the high-error change trials compared with low-error change trials. This was the case even when only correct responses to change trials were considered and failure-to-change errors were excluded from the analysis. Moreover, the effects of error likelihood were seen even on no-change trials, when no second (change) arrow was presented at all. Blue color cues, which came to be associated with a high likelihood of failure-to-change errors, elicited greater activity in the MFC during no-change trials than did white color cues, which were associated with low-error likelihood. The

authors cleverly captured these data together with the observation that MFC activity gradually emerged over the course of the experimental session. They did this by conducting simulations with a nonlinear neural-network model that computationally implemented their assumptions about the prediction of error likelihood. After individuals gradually learned the associations between color cue and error likelihood, presentation of the high-error color cue was sufficient to increase activity in the MFC, even in the absence of other features that might cause conflicting responses or errors (see the figure).

Thus, the MFC determines that goals may not be achieved or rewards may not be obtained unless the level of cognitive control is subsequently increased. This increase in cognitive control takes place not only when a response conflict indicates a reduced probability of obtaining a reward, or when errors signal the loss of an anticipated reward, but also when the context predicts the likelihood of imminent errors (5). Together, these patterns of neural firing confirm that the principal task of the MFC is to monitor performance, that is, to compute and signal the likelihood of obtaining or losing rewards in response to particular actions (10). The MFC thus guides decisions about which actions are worth taking (11). One challenge of the error-likelihood model that needs to be addressed is the incorporation of transient disengagements of MFC activity that foreshadow errors (12). Occasional lapses and other forms of variability are characteristic of all cognitive

processes. Such baroque characteristics should be accommodated in our models of cognitive control as we move beyond the era of the renaissance.

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