Intelligence in action

Matthew V Chafee & James Ashe

The primate prefrontal cortex is associated with cognitive operations linked to intelligence. A study in *Nature* now shows that prefrontal neurons represent movement sequences at an abstract level, even when not required for the task.

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The brain is a sensorimotor interface that in some cases exhibits the elusive property of intelligence. What is intelligence, and how is it implemented by living neurons? One question is at the level of behavior, the other at the level of biology. Both are deceptively simple and yet equally difficult to answer. Their synthesis, if it can be achieved, represents one of the most important and ambitious objectives of neuroscience, and although a workable answer to either question is at least many decades away, recent advances provide tantalizing clues.

Many of these advances have been made by cataloging the cognitive processes supported by prefrontal cortex and characterizing how these functions are implemented by prefrontal neurons. Although intelligence represents the confluence of a variety of processes and capacities, implemented by many neural systems, researchers have had some success in chipping away at this complexity to isolate components of intelligent behavior and relate these to specific neural mechanisms in prefrontal cortex. For example, smart brains plan actions instead of reflexively reacting to the most salient object in the environment. They identify goals and plan sequences of actions to achieve them, and in primates, this ability seems to critically involve the prefrontal cortex. A recent study by Shima, Tanji and colleagues in *Nature*[1] is an important advance in our understanding of how planning abstract sequences of actions may be related to the activity of individual prefrontal neurons.

In this study, monkeys were trained to execute a sequence of movements (**Fig. 1**). They grasped an articulated manipulandum that could be pulled, pushed or turned, so that there were three potential movement elements in a sequence. Monkeys viewed a sequence of visual stimuli that instructed them to execute these movements in a particular order. Each movement sequence consisted of four movements. After a few visually instructed trials, monkeys continued to execute the sequence of four movements without further external instruction. The critical feature of the design was that movement sequences could be classified into one of three categories based on the pattern in which the movements were executed. In the simplest category, monkeys repeated the same movement four times (AAAA). The two more complicated categories involved two different movements performed in different order (ABAB or AABB). Individual exemplars of each sequence category differed in which specific movement(s) were required (push, pull or turn), but shared the same sequential structure of similar versus different actions.

In the interval of time before sequence execution, the authors found that the activity of single prefrontal neurons reflected the category of movement sequence that the monkey intended to perform. Some neurons were activated before movement sequences of the ABAB type, regardless of which specific two movements were required. This neural activity therefore did not differentiate between specific movements but instead encoded the abstract structure of the sequence, irrespective of the serial order or component movements themselves.

Although previous work has shown that prefrontal neurons encode movement sequences, the categorical nature of the representation revealed by the Shima *et al.* study is particularly novel and significant. For example, the activity of prefrontal neurons varies systematically not only with the direction, but also with the serial position of a movement within a sequence[2,3]. This can be considered the most elemental or atomic representation of a sequence. One level above this is the neural representation of a given sequence of movements as a unit[4]. This is akin to a molecular representation of the sequence, as it represents a particular combination of its elements (atoms). The present study adds a third, more abstract layer to this hierarchy of neural representation. In this instance, neural activity is selective for a category of similar sequences that share a rather abstract property—the order in which either one or two movements are made (regardless of the particular movements involved). Abstract representations of action such as this may be crucial to more complex forms of goal-directed behavior. When we plan, for example, it seems we often do it in relatively abstract terms, specifying individual actions conceptually rather than as particular movements. Shima *et al.*[1] provide compelling evidence that prefrontal neurons have a similar capability—they can represent movement sequences as the ordering of abstract actions. Although speculative, it seems that this property of prefrontal neurons may prove essential to our ability to plan action at an abstract level, as opposed to the more basic level at which the metrics of individual movements are specified.

Perhaps the most important aspect of this result is that the task design did not explicitly train the monkeys to generate a categorical representation of the movement sequences. The monkeys were not required to respond differentially as a function of the category to which a given movement sequence belonged, nor were they differentially rewarded on this basis. Therefore, the categorical nature of the task design was not instructed by the reward contingencies that the task imposed. Such a design ensured that prefrontal neurons did not adopt a categorical representation as a byproduct of mapping stimuli to responses within the specific context of the task. On the basis of this finding, we might speculate that prefrontal cortex extracts regularities in events automatically, even when these regularities do not control behavior or predict reward. The ability to extract common and generalized regularities embedded in diverse sequences of events, and to encode these regularities in neural activity, seems of central importance to the processing abilities that make some brains smart. These authors' results therefore provide a biological correlate to at least one intelligent behavior.

These data are consistent with a body of prefrontal research that has implicated this structure in the control of behavior on the basis of internal representations[5]. Pioneering work[6–8] established that prefrontal neurons sustain an elevated firing rate as long as specific items of information are stored in working memory, showing that prefrontal neurons could buffer information pertaining to events in the past[9] or in the future[10]. These findings provided a cellular correlate of the brain's ability to decouple information processing from conditions as they exist in the present moment. This capability is certainly a prerequisite for a brain capable of planning, and it was manifested in the neural activity reported by Shima *et al.* In their study[1],

The authors are in the Brain Sciences Center, Veterans Affairs Medical Center, and Department of Neuroscience, University of Minnesota, Minneapolis, Minnesota 55417, USA.
e-mail: ashe@umn.edu

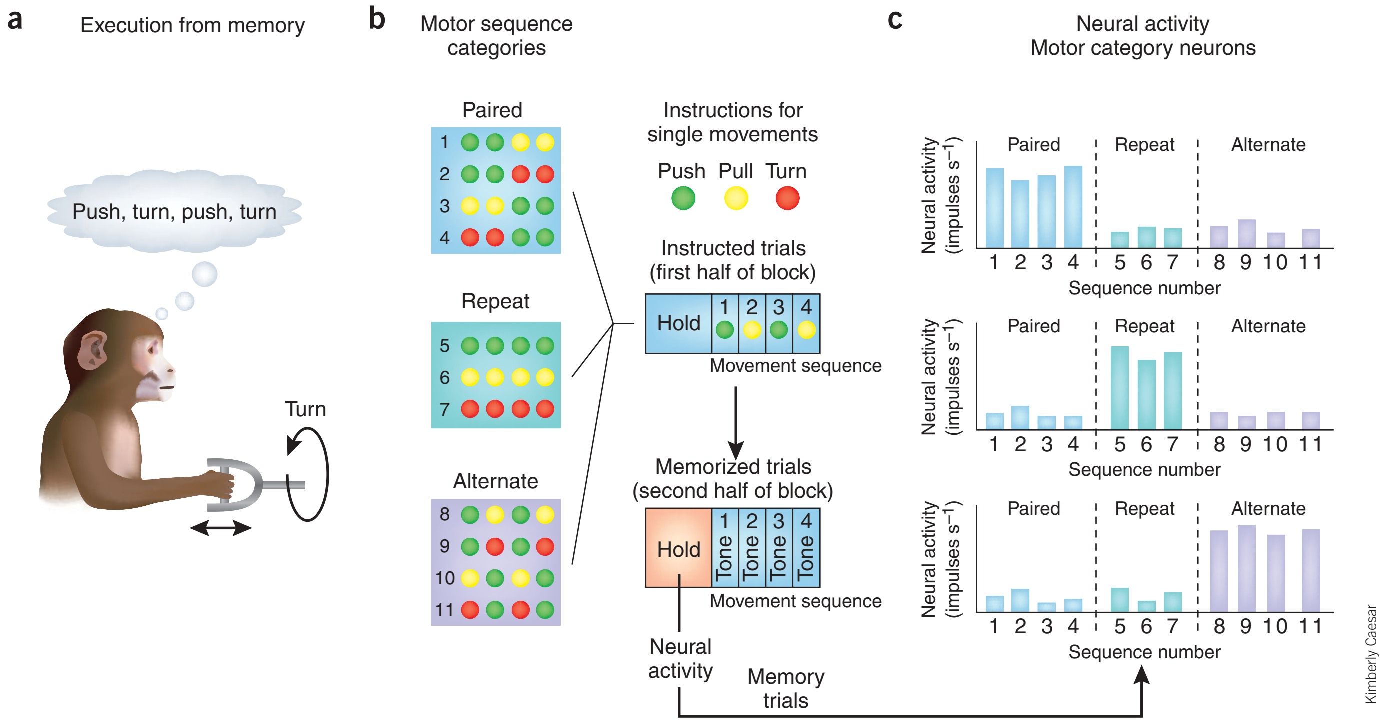

Figure 1 Sequence Task. (**a**) The subjects operated a manipulandum to produce push, turn and pull movements from memory after training. (**b**) Left: the movements were performed as part of a sequence that could be grouped into three abstract categories (paired, repeat, alternate). Right: during training, the movements within a sequence were individually instructed by colored visual stimuli following a long preparatory hold period. (**c**) During the memorized sequence trials, there was no visual instruction and a tone was used as a go signal for each component movement. The neural activity in the preparatory period before the performance of a memorized sequence

prefrontal neurons represented the category of the upcoming movement sequence before it began, and therefore demonstrated temporal independence from current events. Without the capability to disconnect neural processing from the present moment, the brain would be marooned in the present, unable to analyze the past or predict the future, and would therefore be incapable of the foresight that we generally associate with intelligent behavior.

As mentioned above, a critical feature of the results of Shima *et al.* is that their data document the involvement of prefrontal neurons in the categorical representation of action. The ability to categorize events and objects is likely to prove essential to the intelligent control of behavior. By grouping disparate items into a common category, we can acquire generalized knowledge of the world by discovering the properties that apply to all members of a class (such as the knowledge that balls roll and bounce, birds fly, and so forth). It had previously been shown that the activity of prefrontal neurons provides a categorical representation of visual objects[11]. In that study, monkeys were required to classify a visual object as a cat or a dog, when the object in question represented a morph generated by mixing different proportions of cat and dog prototypes. Prefrontal neurons exhibited a preference for the categories 'cat' or 'dog' and abruptly changed their rate of discharge at a midpoint along the morphing continuum from one object shape to the other. This study and the new work from Shima *et al.*[1] are complementary in showing categorical representation in prefrontal cortex in both perception and action planning. In the case of action planning, Shima *et al.* did not show an abrupt change in neural activity at some point along an underlying movement continuum, but the representation seemed to be categorical in so far as neurons were equivalently activated by any of several movement sequences that shared an abstract feature. In the case of perceptual categorization[11], the correct response and reward were defined in relation to the category membership of a given stimulus, so that the categorical representation may have been important in representing task contingencies.

Both studies, and several others demonstrating the involvement of prefrontal neurons in the representation of abstract constructs such as rules[12], decisions[13,14] and numerosity[15], have done much to advance our understanding of how this cortical area may mediate the flexible, adaptive and goal-oriented behavioral control that most people associate with intelligence.

COMPETING INTERESTS STATEMENT
The authors declare that they have no competing financial interests.

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