# Neural Substrates of a Symbolic Action Grammar in Primate Frontal Cortex

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## Abstract

**At the core of intelligence is the capacity to solve new problems. In turn, problem-solving has been hypothesized to depend on cognitive operations resembling symbolic grammars (Newell & Simon, 1976), with two core components: discrete units (symbols) and rules for recombining symbols into new composite representations (syntax). Whether and how symbolic grammars are implemented in neuronal substrates remains unknown. Here, we establish a research program to elucidate the neural basis of action grammars. In a drawing task, macaque monkeys learn action grammars, which guides how they compositionally generalize to draw new images. Our behavioral analyses indicate that these grammars consist of symbolic action primitives and syntactic rules. In recordings of neuronal activity across motor, premotor, and prefrontal areas, we identified separate populations encoding action grammar components, including motor primitives, action symbols, and syntactic rules. Here, we report the discovery of an action symbol representation in ventral premotor cortex (PMv). Specifically, we found that PMv encodes planned stroke primitives, and does so in a manner exhibiting three symbolic properties: abstraction, categorical structure, and recombination. Thus, we have established a paradigm to study compositional generalization using action grammars, and identified a representation of action symbols in PMv. In ongoing work, we are studying how neural activity, in PMv and interconnected areas, may implement the systematic composition of symbols using syntactic rules.**

**Keywords:** compositional generalization; action grammar; action categories, program induction; frontal cortex.

**A compositional drawing task.** Inspired by evidence that drawing involves internal action grammars (Tian et al., 2020), we developed a task in which macaque monkeys draw by tracing novel complex geometric figures **(Fig. 1)**. This task is designed to test internally constructed generalization (i.e., using novel images with no instructive cues), with rich motor behavior revealing underlying cognition, two features which have been lacking in prior drawing-like

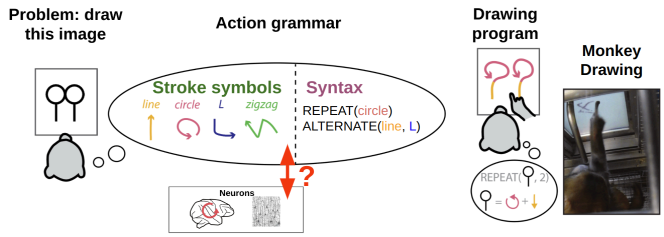


**Figure 1.** Action grammars support compositional generalization in a drawing task for macaques.

and sequencing tasks [e.g., (Averbeck et al., 2003; Shima et al., 2007)].

**Behavioral evidence for action grammars**. Subjects learned and then compositionally generalized action grammars, which consisted of two kinds of components: <u>action symbols</u> (i.e., single-stroke categories, like "circle") and <u>syntax</u> (i.e., sequencing rules, such as "repeat three times") (**Fig. 1**).

**Evidence for action symbols (Fig. 2A-D).** Each subject learned their own set of stroke primitives, given the same images. These strokes exhibit three symbolic properties: they are abstract, categorical, and combinable into sequences. (i) <u>Abstract</u>. Strokes are invariant over motor features like location and size **(Fig. 2A)**, resembling abstraction in human handwriting (Raibert, 1977). (ii) <u>Categorical</u>. Across trials, drawings switch between discrete stroke types, even when images vary continuously (**Fig. 2B,** morphs 1-5), or not at all (**Fig. 2B,** morph 4). (iii) <u>Combinable</u>. Subjects generalize to draw novel complex "character" images by combining their own stroke primitives, even though there are many possible ways these images could have been correctly drawn (**Fig. 2C, D**).

**Evidence for syntactic rules (Fig. 2E, F).** Subjects successfully learned multiple syntactic rules. Two rules include: (i) <u>Repeat shape</u> (e.g., "repeat all circles, then all lines") and (ii) <u>Compound shapes</u> (e.g., "lollipop = line plus circle"). Critically, they generalized these rules even for "extrapolation" images using more lines/circles than in training (**Fig. 2F,** training maxed at 2 lines/circles, but testing was up to 4 lines/circles).

**A neural representation of action symbols**. We recorded simultaneous unit activity across multiple areas of frontal cortex (sixteen 32-electrode arrays**,**

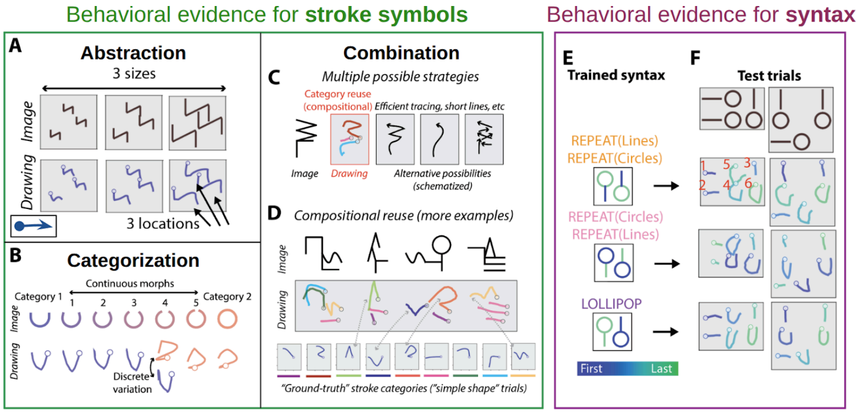


**Figure 2.** Behavioral evidence for action grammar. **(A-D)** Evidence for action symbols. **(E-F)** Evidence for Syntax.

**Fig. 3A)**. We found that PMv, and no other recorded area, encodes stroke primitives during planning in a manner that reflects symbolic properties of abstraction, categorical structure, and combination. (i) Abstraction. PMv activity encodes stroke symbols, invariant to size and location **(Fig. 3B,C)**. This is not true in other areas, which also reflect location or size (see dlPFC, **Fig. 3B,C)**. (ii) Categorization. In tasks where images are morphed between two stroke categories (**Fig. 2B**), population activity in PMv diverges towards two states reflecting the planned stroke category on that trial (**Fig. 3D**, "categ 1/2"). Strikingly, this divergence occurs even for ambiguous images (morph 4), thus reflecting the planned drawing (**Fig. 3D-E**). However, this separation is slower for ambiguous, compared to unambiguous, images (**Fig. 3E**), potentially reflecting winner-take-all competition between stroke categories. (iii) Combination. Activity in PMv encodes strokes similarly between single-shape tasks and multi-stroke "character" tasks, indicating representational "reuse" (Task: **Fig. 2C, D**; Neural: **Fig 3F**). In contrast, activity in a different area (preSMA) differs depending on the task (**Fig. 3F**).

**Conclusions.** Our finding that PMv encodes action symbols (1) provides neural evidence for the existence of a symbolic representation in the brain, which has been hypothesized, but whose empirical support has largely come from behavior and modeling; (2) points to PMV, and not prefrontal cortex, as critical for action-related abstraction (which may account for prior findings of motor invariance and mirror neurons); and (3) is foundational for our ongoing studies of how neural activity supports compositionality and symbolic cognitive operations.

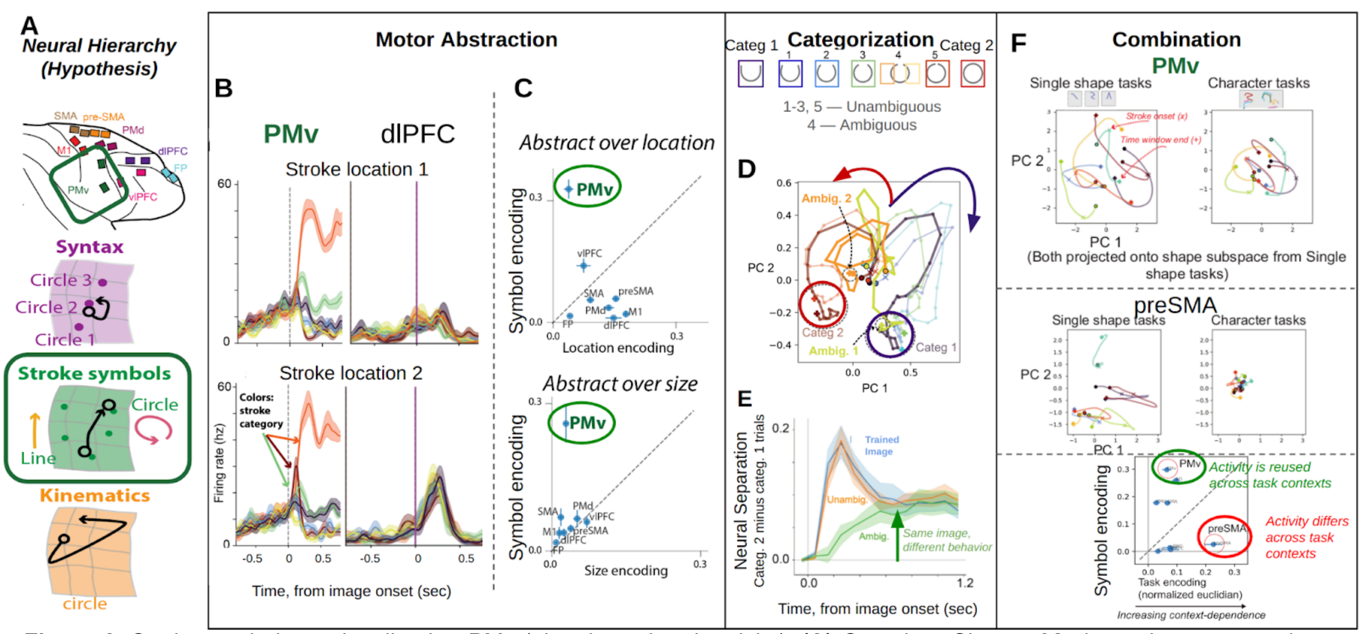


**Figure 3.** Stroke symbols are localized to PMv (planning-related activity). **(A)** Overview. Sixteen 32-channel arrays are shown on brain. **(B)** Example unit activity aligned to image onset, in PMv and dlPFC, grouped by stroke symbol (color) and split by drawing location (rows). PMv encodes strokes similarly across locations. **(C)** Quantification of stroke symbol encoding, euclidean distance between pairs of symbols (population activity), controlling for location. Location/size encodings are defined analogously. **(D)** PMv state space trajectories separate into two categories. "Ambig 1" and "Ambig 2" trials separate based on the planned drawing, given the same image. **(E)** Separation over time. Note slow rise for "Ambig" images. **(F)** PMv encodes stroke category ("shape") similarly when drawn alone ("Single shape" tasks) or in a multi-stroke "character". PreSMA activity is task-dependent. Bottom: Quantification. Shape encoding as in (C); task encoding computed analogously.

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