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Cognitive Imitation in Rhesus Macaques

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Experiments on imitation typically evaluate a student's ability to copy some feature of an expert's motor behavior. Here, we describe a type of observational learning in which a student copies a cognitive rule rather than a specific motor action. Two rhesus macaques were trained to respond, in a prescribed order, to different sets of photographs that were displayed on a touch-sensitive monitor. Because the position of the photographs varied randomly from trial to trial, sequences could not be learned by motor imitation. Both monkeys learned new sequences more rapidly after observing an expert execute those sequences than when they had to learn new sequences entirely by trial and error.

Can a monkey do what a monkey sees? For more than a century, scientists have tried, with little success, to formulate objective answers to this deceptively simple question. Measures of what a student sees while observing an expert perform a task have been poorly defined, as have the criteria for determining which actions count as imitative and which can be explained by the principles of conditioning. These problems reflect definitions of imitation that have relied exclusively on motor tasks. For example, in 1898, Thorndike defined imitation as "learning to do an act from seeing it done" (*1*). A half-century later, Thorpe proposed a more behavioral definition: "copying a novel or otherwise improbable act" (*2*). Although Thorndike's and Thorpe's definitions of imitation have since been qualified and elaborated (*3–5*), neither has been superseded. As a consequence, most research on imitation has focused exclusively on what a subject does at the expense of determining what the subject knows.

Here we describe an example of cognitive imitation, a type of observational learning in which a naïve student copies an expert's use of a rule—for example, learning someone's password at an ATM by looking over the user's shoulder. Because the observer already knows how to enter numbers on the keypad, no motor learning is necessary. The distinction between cognitive and motor imitation is based on the same logic that is used to differentiate cognitive and motor learning in asocial settings (*6*). In the former, the subject must learn to represent external events in their absence—for example, remembering someone's password. In the latter, an external event is available as a cue for the response in question—for example, an expert's motor behavior.

To investigate cognitive imitation, we trained monkeys to execute simultaneous chains, a task in which the subject is required to learn a cognitive rule rather than specific motor actions. The task requires subjects to respond, in a prescribed order, to photographs that are displayed simultaneously on a touch-sensitive monitor (Fig. 1A) (*7*, *8*). Random variation of the positions of the photographs from trial to trial ensures that the subject cannot use a particular motor sequence to execute the task (Fig. 1B) (*9*). Eliminating that possibility was critical; many previously reported instances of imitation in nonhuman primates have been criticized because they may be interpreted as instances of individual learning triggered by the mere presence of a conspecific [social facilitation (*10*, *11*)] or by their interaction with a particular object and/or behavior in a particular location [stimulus/local enhancement (*2–4*)] (*12*).

Simultaneous chains are typically learned by trial and error from feedback that follows each response, correct or incorrect. Correct responses are followed by brief (0.5 s) visual and auditory feedback; errors are followed by a variable (5 to 10 s) time-out, during which the screen is dark. Subjects received a food reward only after they responded correctly to all four items on the monitor ($A \rightarrow B \rightarrow C \rightarrow D$) (*9*). A trial ends either when the subject responds incorrectly to an item or when the subject responds correctly to all of the items on the screen. On a four-item list, the probability of a subject guessing the correct sequence on the first trial and thereby earning a food reward is $1/4! = 0.04$.

In the current study, two monkeys were each provided with the opportunity to learn new lists by cognitive imitation rather than by trial and error. On those lists, one monkey was designated as the "expert," the other as the "student." The expert had previously learned to execute the target list at a high level of proficiency. The student had no prior experience with the target list but was allowed to observe the expert execute that list before testing (*13*). Learning a list in this manner is much more difficult than learning someone's password at an ATM by looking over the user's shoulder, because on an ATM the spatial positions of the number buttons never change.

Our subjects were two male rhesus macaques, Horatio and Oberon. Both subjects had acquired considerable expertise at learning lists by trial and error in previous experiments (*8*). In the present study, subjects learned to execute 70 different four-item lists of arbitrarily selected photographs in two adjacent sound-attenuated chambers. The interior walls of each chamber contained a window made of tempered glass. When an opaque partition was placed between the

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booths, each glass wall functioned as a mirror. When the partition was removed, subjects had a full view of one another (*9*).

In experiment 1, each subject was tested on 30 four-item lists. Fifteen of those lists were collected in isolation with the partition between the chambers in place (baseline condition). Baseline performance provided a measure of trial-and-error learning. On the remaining 15 lists, the partition was removed (social-learning condition). This allowed a naïve monkey (the student) to observe an experienced monkey (the expert) execute the list on which the student would be tested. Baseline and social-learning lists were alternated during successive sessions to balance any list-learning expertise that subjects might develop while learning new lists under each condition (*9*).

Under the social-learning condition, the expert and the student were placed in their respective chambers at the same time before the start of each session. The expert performed a list on which he had been overtrained [mean accuracy for Horatio = 75.5%; Oberon = 78.7%] (*13*). The student was introduced to that same list during two successive blocks of 20 trials. During the first block of 20 trials, the expert executed the overlearned list (observation period). Throughout this block the student's monitor was dark and inactive. That arrangement allowed the student to observe, but not perform, the sequence that the expert was executing in the adjacent chamber. During the second block of 20 trials (test period), the student's monitor was activated. This was the student's first opportunity to respond to the new list items. The onsets of each of the expert's and the student's trials were completely independent. The student and the expert worked side by side throughout the test period, in full view of each other, until the student completed his block of 20 trials (*9*).

A monkey capable of cognitive imitation should acquire a new list more rapidly when watching an expert execute that list than when learning a new list entirely by trial and error. Our measure of cognitive imitation was the number of responses a subject made on a new list before completing his first trial correctly. This is a very sensitive measure of cognitive imitation because, after the first correct trial, a subject's performance may be influenced by cognitive imitation, by trial and error, or by both factors.

As seen in Fig. 2A, Horatio and Oberon benefited substantially from observing an expert execute a list before being tested. Subjects made significantly fewer responses before completing their first trial correctly under the social-learning condition than under the baseline condition. That difference suggests that students learned some of the new list items vicariously by monitoring the responses of the expert during the social-learning condition.

To justify that conclusion, it is necessary to control for two factors that may have favored list learning under the social-learning condition. In experiment 2 we sought to control for nonsocial learning. In this instance, a student could benefit from the social-learning condition even if he ignored the presence of the expert in the adjacent chamber. To learn the serial position of items in a new list, the student only needed to attend to the visual and auditory feedback that followed each of the expert's correct responses. In experiment 3, we sought to control for social facilitation that could have resulted from the mere presence of the expert monkey in the adjacent chamber (*10*, *11*). Under this scenario, social facilitation would have increased the student's motivation to attend to the consequences of responding to each list item. In experiments 2 and 3, students had the same view of the adjoining chamber that they did under the social-learning condition in experiment 1. Each session consisted of a 20-trial observation block followed by a 20-trial test block.

In experiment 2, the chamber that was previously occupied by the expert monkey was empty and a computer simulated an expert's performance on the list on which the student was tested (computer-feedback condition). In experiment 3, the expert and the student worked side by side on different lists (social-facilitation condition). Subjects learned 20 new lists in each experiment: 10 under one of the control conditions and 10 under the baseline condition (*9*).

Neither control condition enhanced list learning. The number of responses students needed to complete their first correct trial under the social-facilitation and the computer-feedback conditions did not differ from the number of responses needed during the baseline conditions (*9*).

Having established that the social-learning condition was the only condition under which list learning was enhanced, we sought to clarify what the student learned from the expert. From experiment 1, we know that a subject in the social-learning condition did not learn the positions of all of the items by observing an expert execute a new list. If that were the case, the student would have needed, on average, only four responses to complete his first correct trial (Fig. 2A).

What the student gleaned from the expert's performance was revealed by an item-by-item analysis of the relative frequency of a correct response at each position of the sequence before the completion of the first correct trial on a new list. This analysis revealed that, in the social-learning condition, Horatio and Oberon learned the ordinal position of at least two list items. Horatio's accuracy when responding to items A and D and Oberon's accuracy when responding to items B and C exceeded, by at least 20%, their

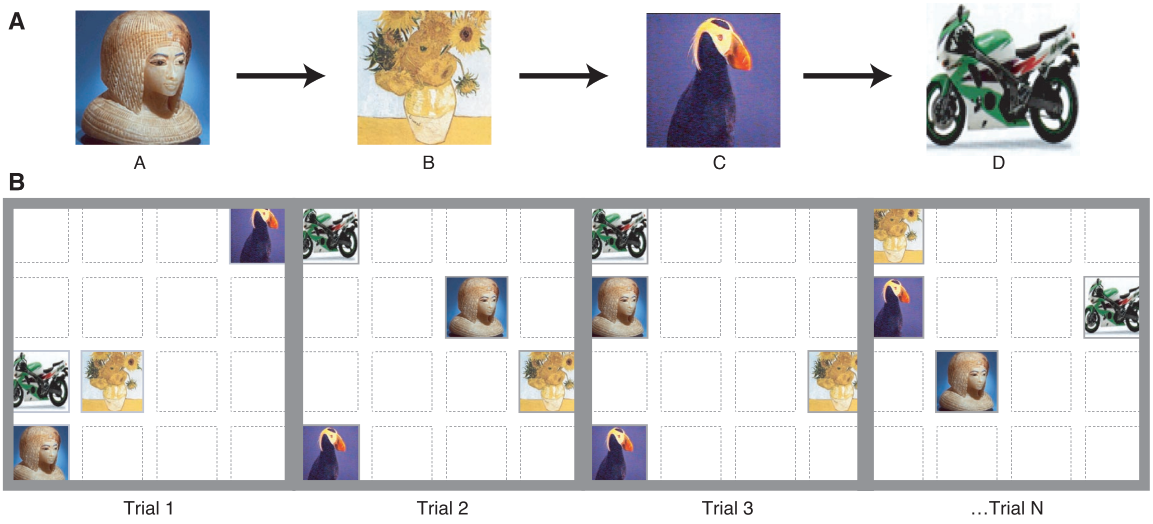

Fig. 1. Simultaneous chaining task. (**A**) Sample of four-item list of arbitrary pictures. (**B**) Example of how list items (pictures) change spatial configuration from trial to trial.

accuracy when responding to items in these positions under the baseline and the two control conditions (*9*).

At this stage of our research, we attach no importance to our subjects' idiosyncratic selection of the items learned while observing an expert execute a list. Those differences notwithstanding, the specific ordinal knowledge that Horatio and Oberon acquired as students was equally effective in minimizing the overall number of errors in the social-learning condition. Knowledge of the ordinal positions of any two items makes it easier to infer the ordinal position of the remaining items by trial and error.

It remains to be seen whether a student could learn a new list without making any errors by observing an expert execute that list. The fact that Horatio and Oberon did not achieve that level of expertise should not, however, detract from the threefold implication of the cognitive imitation that they did display. Foremost, Horatio and Oberon's performance as students in the social-learning condition demonstrates cognitive imitation in an animal. Second, their performance challenges the widely held view that apes are the only animal species capable of learning by imitation (*4*, *5*, *14–16*). Third, Horatio and Oberon's performance falls outside the scope of all current theories of social learning (*2–5*, *12*, *17–24*).

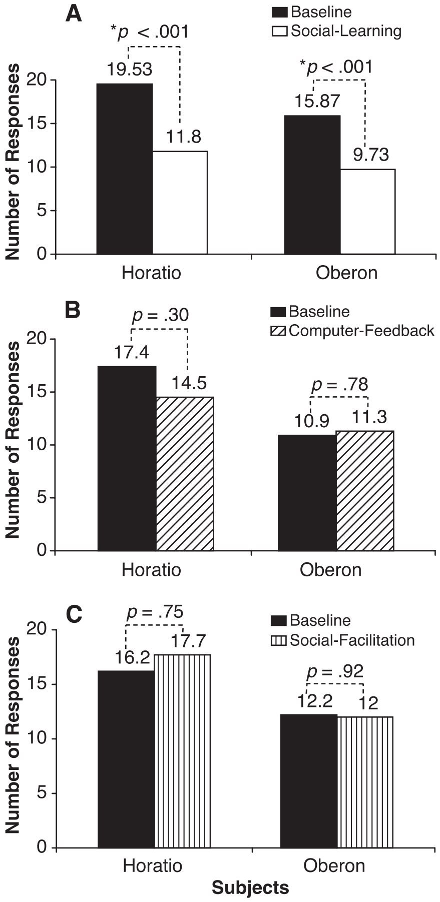

Fig. 2. (**A**) Summary data of experiment 1: cognitive imitation [Horatio: $t(29) = 8.20$, $P < 0.001$; Oberon: $t(29) = 9.39$, $P < 0.001$, two-tailed paired-samples *t* test]. (**B**) Summary data of experiment 2: computer-generated feedback [Horatio: $t(9) = -1.11$, $P = 0.30$; Oberon: $t(9) = 0.28$, $P = 0.78$ (two-tailed paired-samples *t* test)]. (**C**) Summary data of experiment 3: social facilitation [Horatio: $t(9) = 0.34$, $P = 0.75$; Oberon: $t(9) = -0.11$, $P = 0.92$ (two-tailed paired-samples *t* test)].

The ability of Horatio and Oberon to acquire ordinal information by observing an expert execute a list stands in strong contrast to the failure of other experiments investigating imitation in monkeys (*21*). The current experiment differs from previous studies in many respects. Of greatest importance, our paradigm allows for the separation of motor and cognitive rules, the execution of which might contribute independently to imitation learning. Indeed, this is the only experiment on imitation of which we are aware in which no motor learning was necessary. The use of a familiar motor task throughout testing, in this instance the simultaneous chaining paradigm, also made it possible to obtain multiple observations of imitation from the same subject.

The simultaneous chaining paradigm also made it possible to demonstrate evidence of cognitive imitation even when a subject did not reproduce a list perfectly (table S2). By contrast, experiments on motor imitation must focus on a single trial. Failure to reproduce the expert's performance on the first trial counts as a negative result because, on subsequent trials, it is not possible to separate what was learned by observation from what was learned by trial and error. An equally serious problem is the subject's level of motor sophistication. Consider, for example, the outcome of an experiment, like this one, in which progress on a cognitive task presupposes knowledge of the motor task. The likelihood that subjects could learn either type of task by imitation is nil.

Theories of stimulus or local enhancement cannot explain how Horatio and Oberon acquired ordinal knowledge of at least two items on social-learning lists. At best, those theories can offer an account of how a student might learn the first or the last item of a new list because these items would be the most salient. Under this scenario, the expert would draw the student's attention to one of these two items. The student would then search for that item on his own video monitor (while ignoring the remaining items on the screen, with the added difficulty that the item's location differs from the location on the expert's screen). Theories of stimulus or local enhancement cannot, however, explain how students could acquire knowledge of the ordinal positions of items B or C because they make no provision for learning serial rules.

Theories of social facilitation and stimulus enhancement would predict, respectively, more rapid list learning under the social-facilitation and the computer-feedback conditions than under the baseline condition. None occurred. Theories of emulation learning [e.g., (*4*, *5*, *16*, *17*, *24*)] cannot explain the type of cognitive imitation measured here because the simultaneous chaining paradigm does not provide any "affordances" or any causal relationship between individual list items. Because all new lists consisted of arbitrarily related pictures, subjects could not use a general ordering rule between lists. Instead, subjects had to develop a unique ordering rule to execute each new list.

Our evidence of cognitive imitation in monkeys is consistent with recent hypotheses about different "levels" of imitation [e.g., (*14*, *15*, *18*, *25–27*)]. For example, Whiten (*25*) and Byrne (*26*) have each argued that a student may copy specific actions of a model ("action-level imitation") or that a student may copy the underlying structure and/or goal of observed motor movements ("program-level imitation"). In this experiment, the program our monkeys imitated was one that allowed them to identify the ordinal position of new list items.

Having empirically isolated cognitive imitation from motor imitation, we are left with many questions. First, although subjects that fail motor imitation tasks may succeed on cognitive imitation tasks, we cannot state the necessary and sufficient conditions for cognitive imitation to occur. Second, little can be said about either the evolutionary history of motor and cognitive imitation or their underlying neural mechanisms. As a result, we cannot hypothesize about the extent to which other species may learn by cognitive imitation.

There are, however, two findings—one from this experiment, and one from experiments on responses of individual cells from a monkey's cortex—that suggest some strategies for addressing these questions. In this experiment, the expert's eye-hand coordination, as it moved from one item to the next on the same list that was presented to the student, may have recruited the student's attention to the ordinal position of those items. That aspect of the social-learning condition was absent in both the computer-feedback and social-facilitation conditions. The salience of the expert's actions while responding to particular items in the social-learning condition may be similar to that observed in experiments that reported the firing of specific neuron populations in the inferior frontal and medial temporal lobes of monkeys that observed intentional movements executed by a trainer or by another monkey (*28*, *29*). It would, therefore, be of interest to explore the extent to which those neurons contribute to cognitive imitation.

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12. Stimulus, local enhancement, and social facilitation are terms that refer to specific instances of individual learning that are triggered by the activity of a conspecific. Stimulus and local enhancement occur because the model's behavior attracts an onlooker's attention toward some object or some activity in a location. Social enhancement refers to an increase in attention and motivation when engaged in a task that occurs in the presence of another individual. Without experimental controls, it is unclear whether the onlooker who later approaches and interacts with the object in question copied the model's action, or instead learned to produce the same behavior by individual trial-and-error learning. Observers may also learn about the causal structure of actions by observing a model. For example, an individual who watches a model use a rake to reach a food item may learn that the rake may be used to attain out-of-reach food, but not that there is a specific technique for using rakes. This mode of social learning, where subjects learn the causal relationship between an object (e.g., a tool) and a desired outcome (e.g., food), has been described as the "emulation of affordances" or emulation learning (*4*). However, Whiten and Ham (*5*) have argued that individuals in these studies may be copying the goals of the model (not necessarily their specific techniques). As a result, these authors prefer to call this mechanism "goal emulation."
13. Both Horatio and Oberon each served as a "student" and as an "expert." Experts were trained in isolation (with the partition dividing the two chambers) until they completed at least 65% of the trials correctly during two consecutive sessions.
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Supporting Online Material

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Materials and Methods

Figs. S1 to S3

Tables S1 and S2

Movie S1

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