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Research report

Learning by observation in the macaque monkey under high experimental constraints

Faiçal Isbaine[a], Marie Demolliens[a], Abdelouahed Belmalih[b], Andrea Brovelli[c], Driss Boussaoud[a,*]

[a] Institut de Neurosciences des Systèmes, INSERM U1106, Aix-Marseille University, Marseille France
[b] Stem cells and Brain Institute, 18 avenue du Doyen Lépine, 69500 Bron France
[c] Institut de Neurosciences de laTimone, UMR7289, CNRS & Aix-Marseille University, Marseille France

HIGHLIGHTS

- We have examined observational learning in two macaque monkeys under the constraining experimental conditions of behavioral neurophysiology.
- Monkeys can learn by observation both from a conspecific and the experimenter, even under such conditions, thus opening the way for electrophysiological studies.
- Learning by observation is better after observation of errors than from successes.

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ABSTRACT

While neuroscience research has tremendously advanced our knowledge about the neural mechanisms of individual learning, i.e. through trial-and-error, it is only recently that neuroscientists have begun to study observational learning, and thus little is known about its neural mechanisms. One limitation is that observational learning has been addressed under unconstrained experimental conditions, not compatible with neuronal recordings. This study examined observational learning in macaque monkeys under the constraining conditions of behavioral neurophysiology. Two animals sat in primate chairs facing each other, with their head fixed. A touch screen was placed face up between the chairs at arm's reach, and the monkeys were trained on an abstract visuomotor associative task. In one experiment, the monkeys alternated the roles of "actor" and "observer". The actor learned to associate visual cues with reaching targets, while the observer "watched" freely. Then, the observer was given the same cue-target associations just performed by the actor, or had to learn new, not previously observed ones. The results show that learning performance is better after observation. In experiment 2, one monkey learned from a human actor who performed the task with errors only, or with successes only in separate blocks. The monkey's gain in performance was higher after observation of errors than after successes. The findings suggest that observational learning can occur even under highly constraining conditions, and open the way for investigating the neuronal correlates of social learning using the methods of behavioral neurophysiology.
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1. Introduction

Learning by observation allows individuals to acquire information and to learn new skills using others' negative and positive experience [1]. Since the beginning of the 20th century, researchers have shown interest in understanding how behavior of an individual may change as a result of observing conspecifics, or members of other species. The ability to learn from others is present in many animal species including birds [2–5], fish [6,7], and mammals [8–10]. In primates, Darby and Riopelle [11] have conducted the first controlled study where monkeys watched a conspecific performing an object-discrimination task, and found that the observer gained in performance following observation. Interestingly, this study was also the first to show that observation of erroneous trials was more beneficial than correct trials. More recent studies have confirmed these early findings using a variety of tasks and experimental conditions in different non-human primate species including capuchins, macaques, baboons and chimpanzees [10,12–20].

* Corresponding author. Tel.: +33 622263752 ; fax: +33 491789914.
E-mail addresses: driss.boussaoud@univ-amu.fr, driss.boussaoud@gmail.com (D. Boussaoud).

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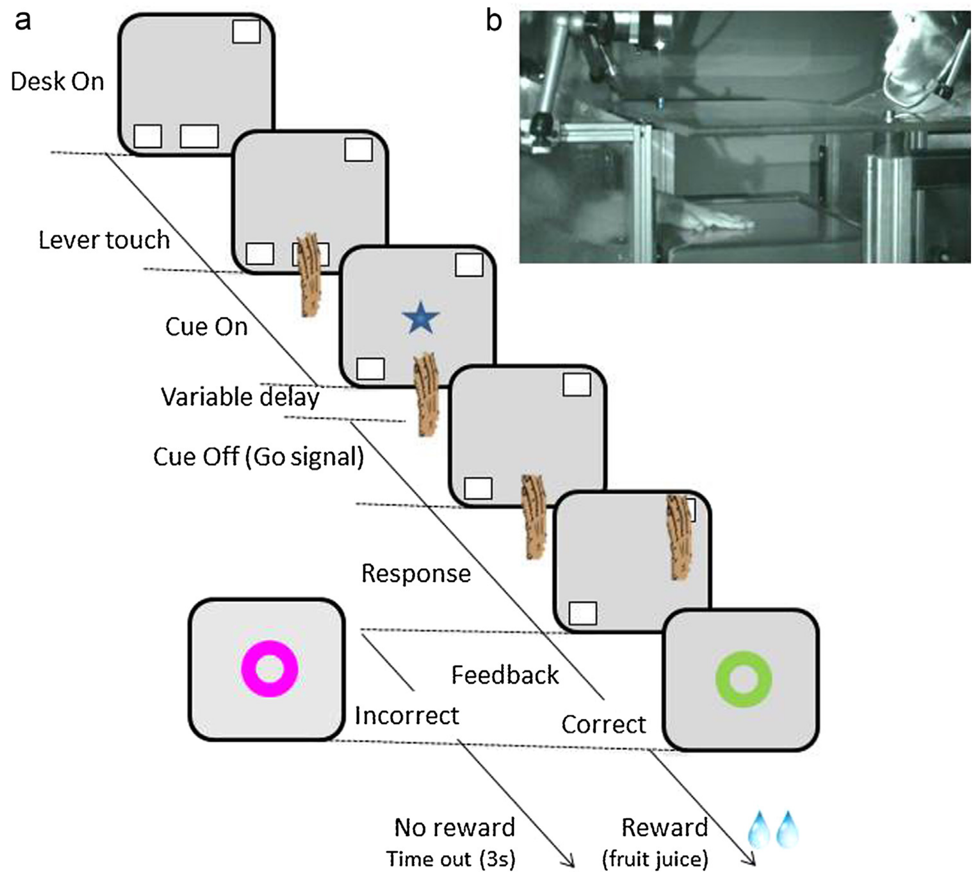

Fig. 1. Behavioral task. *a. Main steps of the task.* The successive grey squares represent the touch screen located between the two monkeys (b) from the start of a typical trial (top) to its end (bottom). A trial starts (top) with onset of 2 white squares (targets) and a rectangle (lever), together termed "desk". The monkey had to initiate the trial by touching the lever. The detection of the level touch by the computer software triggered the onset of a central cue (a star in this example), which remained on the screen for a variable delay. Offset of the cue served as the go signal, instructing the monkey to touch one of the two targets. If the target choice was correct, a green annular appeared to indicate a correct response (positive feedback), and a reward (drops of fruit juice) was delivered after 1 s to the actor. If the touched target was not the one associated with the cue, a purple annular appeared (negative feedback) and no reward was given. b. Photo of the setup. The photo shows the observer and the actor's hand on the lever.

Whereas neuroscience research has intensively studied the neuronal mechanisms of learning through trial and error (TE) during the last 2 decades (e.g. [21–25] and [26] for review), it is only recently that neuroscientists have begun to investigate observational learning, and thus little is known about the neuronal correlates of this type of learning [27,28]. One main limiting factor might be, from the behavioral perspective, that observational learning has so far been examined using ethological and psychological approaches. Indeed, previous studies (reviewed above) have used experimental conditions with limited constraints. On the other hand, it is technically challenging to record neuronal activity in such conditions, and to repeat the measures under similar trials in order to correlate neuronal activity and behavioral variables. One possibility is to take the observational learning paradigm into the neurophysiological laboratory, and adapt it to the constraints typical of behavioral neurophysiology environment. We have thus undertaken this work to examine whether monkeys can still benefit from observation while sitting in a primate chair, with the head fixed, and when they have to learn an abstract task (as opposed to manipulating real objects), with a reward delivered as the ultimate outcome of a sequence of events. If observing an actor under these conditions still improves the learning performance, as compared to trial-and-error learning, would it follow similar rules as those reported in more ecological conditions? To this aim, we developed a social version of the visuomotor conditional associative task typically used to investigate the neuronal correlates of learning. In one experiment, two monkeys learned one from another, alternating between the roles of actor and observer. We found that their learning performance, i.e. learning rate, was faster following observation as compared to TE learning. In a second experiment, we found that a monkey can learn from a human actor, and that learning from the model's errors was better than learning from correct trials.

2. Material and methods

2.1. Animals

Two male Rhesus monkeys (monkey (A), 12 kg; monkey (M), 11 kg) were the subjects in this study. They were housed together since the age of 3 years, i.e. from the start of the study, in order to allow them to establish stable and spontaneous social interactions. Animal care, housing and experimental procedures conformed to the European Directive (2010/63/UE) on the use of nonhuman primates in scientific research.

The two monkeys were maintained on a dry diet for the duration of the study. Their liquid consumption and their weight were carefully monitored on a daily basis early in their training, and on a weekly basis during the steady phase of the experiment.

2.2. Behavioral paradigms: general design

The two monkeys were tested together on a daily basis. Each of them sat in a primate chair facing each other with a touch screen between them at arm's reach (Fig. 1). A sliding door placed in front of the chair allowed (or prevented) access to the touch screen. Only

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