



Rats' learning of a new motor skill: Insight into the evolution of motor sequence learning

Linda Hermer-Vazquez*, Nasim Moshtagh

Behavioral Neuroscience Program, Psychology Department, University of Florida, Gainesville, FL 32611, United States

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ABSTRACT

Recent behavioral and neural evidence has suggested that ethologically relevant sub-movements (movement primitives) are used by primates for more complex motor skill learning. These primitives include extending the hand, grasping an object, and holding food while moving it toward the mouth. In prior experiments with rats performing a reach-to-grasp-food task, we observed that especially during early task learning, rats appeared to have movement primitives similar to those seen in primates. Unlike primates, however, during task learning the rats performed these sub-movements in a disordered manner not seen in humans or macaques, e.g. with the rat chewing before placing the food pellet in its mouth. Here, in two experiments, we tested the hypothesis that for rats, learning this ecologically relevant skill involved learning to concatenate the sub-movements in the correct order. The results confirmed our initial observations, and suggested that several aspects of forepaw/hand use, taken for granted in primate studies, must be learned by rats to perform a logically connected and seemingly ecologically important series of sub-movements. We discuss our results from a comparative and evolutionary perspective.

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1. Introduction

Since Wolfgang Kohler's famous experiments on chimpanzee problem solving and "insight" (Köhler and Winter, 1926), comparative psychologists have questioned Kohler's experimental interpretations and have investigated similar, apparently insight-driven motor learning processes with greater scientific rigor (Chance, 1960; Epstein et al., 1984; Windholz, 1984). In one of the most oft-cited experiments, Kohler placed a banana hanging from the ceiling beyond the chimpanzees' reach. After failing to obtain the banana by jumping from the ground, some chimps appeared to sit quietly for a moment, then would jump up and pile crates from a distant part of the room on top of one another under the fruit, creating a sort of stepping stool that allowed them to grasp the prize. Although Kohler argued that the chimps' learning process involved genuine insight, further experiments with chimps, pigeons and other species have instead supported the notion of a learning process based on prior Pavlovian and operant conditioning, and Thorndikian trial-and-error learning (Epstein et al., 1984; Windholz, 1984). Thus, Kohler's "insight" experiments are more accurately described as motor sequence learning in pursuit of a goal.

During the learning process, however, Kohler's chimps and the other animals seldom if ever performed the steps toward eventual success in a disordered manner. For instance, a chimp did not fail to

grasp a banana, yet still bring its hand to its mouth and begin chewing. Though it may seem surprising that we would even comment on this, in our extensive experience with *rat* motor skill and motor sequence learning (Hermer-Vazquez, 2008; Hermer-Vazquez et al., 2004, 2007a,b), we have often seen the animals perform such movements strangely out of order—indeed, including failing to grasp a pellet during a reaching task and yet bringing their reaching paw to their mouths, sometimes with subsequent chewing. Gharbawie, Whishaw and colleagues (Gharbawie et al., 2007; Gharbawie and Whishaw, 2006) have noticed some of the same tendencies of rats learning the same skilled reaching maneuver both *before* and after cortical injuries.

In contrast, when non-human primates are learning a new motor skill, they appear to do so by concatenating simpler movements – such as extending the forearm, defending the face with the hand, grasping an object, or bringing the hand to the mouth while holding an object – in the correct order from the start (Rizzolatti and Luppino, 2001). These sub-movements are often referred to as movement primitives and have been studied extensively at the behavioral and neural levels (Cooke and Graziano, 2003; Graziano, 2006; Graziano et al., 2002a,b; Stepniewska et al., 2005). At the beginning of both ecologically relevant and, to some degree, arbitrary motor sequence learning, adult monkeys, chimpanzees and humans perform the new, more complex movements in a hesitant fashion, but almost always with correct ordering. Furthermore, they rapidly come to link the primitives or arbitrary steps into a whole, longer and more complex skill (Averbeck and Lee, 2007; Averbeck et al., 2006; Barone and Joseph, 1989; Hodgson et al., 2000; Ninokura

* Corresponding author. Tel.: +1 352 273 2172; fax: +1 352 392 7985.
E-mail address: lindahv@ufl.edu (L. Hermer-Vazquez).

et al., 2004; Shima et al., 1996). Similarly, from the time of reaching onset (~5 months) human infants have been shown to efficiently coordinate proprioceptive, visual and motor information into relatively smooth and correctly ordered sequences of steps to grasp visually detected objects, in both ecologically valid and more arbitrary and laboratory-set tasks (e.g. Barrett et al., 2008; McCarty et al., 2001). Obviously, however, humans and other primate species tested in the highly arbitrary tasks required some degree of trial-and-error learning (e.g. Averbeck and Lee, 2007; Averbeck et al., 2006; Hikosaka et al., 1999; Rand et al., 2000).

It has not yet been shown that rats possess movement primitives similar to those of primates (whether learned, innately encoded, or a combination of both), although there is some suggestion of it from studies of rats' food handling (Ivanco et al., 1996). Nor has it been demonstrated quantitatively that their learning in otherwise well-studied reach-to-grasp-food task (Gonzalez et al., 2004; Hermer-Vazquez, 2008; Hermer-Vazquez et al., 2004, 2007a,b; Hyland, 1998; Jarratt and Hyland, 1999; Kleim et al., 1998, 2002; Whishaw et al., 2003; Whishaw and Pellis, 1990), or any other type of motor skill, proceeds from sequences of disordered movement primitives to a correctly ordered and smoothed sequence. In primate studies cited above, the more ecologically valid a task appears to be, the more a correct ordering of movement steps is present from initial task learning. In the two experiments we present here, a group of rats performed the reach-to-grasp-food task that is considered to be at least semi-natural: for instance, it has been shown that rats use their forepaws to reach for food of the size used here, and can reach through slots or onto shelves to do so (Whishaw et al., 1992). In Experiment 1, we quantitatively and qualitatively analyzed rats' learning of the skilled reaching task in detail. In Experiment 2, we compared the sequence ordering during skilled task learning to that of a second group of rats learning an arbitrary, experimenter-determined sequence of movements. Our findings indicate that rats appear to possess at least some of primates' movement primitives, and that their learning of the (at least partly) ecologically valid skilled reaching task proceeds from certain types of disordered sub-movement sequences to a correctly ordered sequence. We also found that their learning of the correct ordering occurs at a rate similar to that of animals in the arbitrary-sequence task, suggesting that rats, unlike primates, must learn to concatenate movement primitives in a logical and successful order.

2. Materials and methods

2.1. Subjects

We used 10 adult female Long-Evans rats, age ~4 months on arrival and weighing ~270–300 g. All housing conditions and procedures were approved in advance by the university's Institutional Animal Care and Use Committee (IACUC). The rats were housed in pairs in a reversed light-cycle, 12:12 h dark/light room in the department's animal facility. Before starting the experiments, we restricted the rats' food intake, gradually reducing their body weight to 85–90% of their ad libitum weights. During this time (~2 weeks), we handled them for approximately 10 min/day. After the rats attained a stable, food-restricted weight, they were randomly assigned to either the skilled movement group, to be used in Experiments 1 and 2, or the arbitrary-sequence group, whose motor sequence learning was compared to that of the skilled group in Experiment 2.

2.2. Apparatus

The testing apparatus for the skilled task was made of clear Plexiglas with dimensions of 13.1 cm wide × 40 cm deep × 45 cm high (as

in Whishaw and Pellis, 1990 and Hermer-Vazquez, 2008; Hermer-Vazquez et al., 2004, 2007a,b). The box stood on a plastic table with clean paper towels covering the floor for each rat. The front wall of the box had a slot 10 cm high and 1.2 cm wide through which the rats could reach for a food pellet. The shelf on which the food pellet rested had two small wells 1.3 cm beyond the slot, where the food pellets were placed, just beyond the reach of most rats' nostrils and tongues. The real pellets used for the GO trials in both experiments were banana-flavored and 45 mg and 4.2 mm in diameter (Bioserv Inc., Frenchtown, NJ). The artificial, plastic-scented beads used on control, NO-GO trials, to determine whether rats' reaching was olfactory guided, were 4.1 mm in diameter and virtually visually identical to the food pellets. (These same beads were used in a study of the sensory guidance of rats performing the skilled task used here; Hermer-Vazquez et al., 2007a,b.)

For the control, arbitrary-sequence task, a standard MedAssociates rat operant chamber (MedAssociates, St. Albans, VT) was used, which contained a house light, olfactometer, nose port, lever, and a pellet magazine. On each trial, the rats in this group sniffed either a GO or a NO-GO odor inside a standard rat nosepoke hole, and on GO trials were to press a lever approximately 7.6 cm to the rat's right. Programs for the training stages and final control task were written in standard Med-PC programming language.

2.3. Video recording and analysis

The animals were videotaped using a Super VHS video camera (Panasonic, USA) at 30 frames/s. Rats that were comfortable performing the task in regular room lighting were videorecorded with the lights on, whereas more anxious rats were tested under low-luminance red lighting. Recordings were coded using a motion-analysis VCR and with a coach's remote (Lafayette Instruments, Lafayette, IN). The field-by-field display function of this VCR allowed us to code the rats' movements at 17 ms resolution.

2.4. Procedure

2.4.1. Skilled motor task

This task was a discriminant responding procedure, with odor-guided GO and NO-GO trials. At the beginning of training, each rat was placed in the box and given time to discover that several pellets were resting on the shelf beyond them. They were allowed to reach for a food pellet with their limb of preference. Once they sufficiently displayed their handedness, pellets were placed in the well contralateral to their reaching paw and videotaping began. Pellets were replaced when the rat retrieved and consumed the food or displayed an unsuccessful reach, immediately after which the pellet was pushed away or removed. Daily sessions concluded when the rat lost motivation and no longer attempted to reach (usually after 50–100 motivated trials). On approximately 15% of trials, an artificial plastic bead was placed in the contralateral pellet well, or with the real food pellet placed in the ipsilateral well or between the two wells but farther away from the rat, to keep the initial sniffing phase necessary (because the pre-reaching sniffs are used to determine the endpoint of the reaching trajectory Hermer-Vazquez et al., 2007a,b). Training ended with 3 days of level performance, defined as an asymptote in the percent of correct reaches (on which the percentage of correctly ordered reaching sequences did not differ by more than 5% of the running asymptotic mean). Additionally, following the last day of training, each rat was tested for 20 trials with a plastic, visually similar bead in order to confirm that the reach was olfactory guided. The video recordings of each rat were later analyzed and scored based on their sequence of movements to retrieve a pellet.

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