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Observational learning of a spatial discrimination task by rats: learning from the mistakes of others?

Tiaza Bem [a], Bartosz Jura [a], Bruno Bontempi [b, c, 1], Pierre Meyrand [b, c, *, 1]

[a] Nalecz Institute of Biocybernetics and Biomedical Engineering, Polish Academy of Sciences, Warsaw, Poland
[b] Institut des Maladies Neurodégénératives, Université de Bordeaux, UMR 5293, Bordeaux, France
[c] CNRS, Institut des Maladies Neurodégénératives, UMR 5293, Bordeaux, France

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Learning by observing others has been acknowledged as a powerful learning strategy. Whereas in several species observation of fear conditioning or other operational procedures can improve subsequent performance during actual learning, much less attention has been paid to observational learning of spatial discrimination tasks. To this end, we developed a set of procedures in which the spatial memory of adult rats, *Rattus norvegicus*, was tested in an eight-arm radial maze. Moreover, in view of controversial information concerning the incidence of mistakes made by demonstrators on the effectiveness of observational learning, our observer rats watched experienced or nontrained demonstrators. Food-deprived observers and demonstrators were initially habituated to the maze with all arms baited. Then observers were placed in a mesh cage positioned above the maze while a demonstrator rat was locating the spatial position of three baited arms. Rats observing conspecifics progressively learning the spatial discrimination improved subsequent performance compared to a control group watching an empty maze, but only if the configuration of baited arms presented during demonstration and testing matched. Therefore, rats integrated relevant spatial information during observation and used it efficiently when their spatial discrimination was tested in the maze. However, when the information was provided by trained demonstrators, making no mistakes and visiting only baited arms, observer rats failed to exhibit improved performance. Nevertheless, when given an initial habituation without food rewards, rats were subsequently able to benefit from observation of trained demonstrators thus showing that watching mistakes was not necessary for successful observational learning. Together, these findings indicate that rats can acquire spatial information via observation enabling more pertinent search strategies during testing and that for observation to be beneficial, what is observed must be sufficiently relevant or novel to complement existing knowledge (here initial habituation with or without rewards).

In humans and other animals, from invertebrates to primates, new behaviours may be learned through observation of others' experience. Learning by observation has been shown to be crucial in many adaptive behaviours like foraging, predator avoidance, mating decisions, fear learning and problem-solving strategies (Galef & Laland, 2005). Such learning allows the animal to save energy and time by circumventing costly trial-and-error learning or avoiding the threat of an adverse situation. Observational learning (OL) has been reported in invertebrates such as octopus (Fiorito & Scotto, 1992), social insects (Avarguès-Weber & Chittka, 2014; Loukola, Perry, Coscos, & Chittka, 2017; Worden et al., 2005) and nonsocial insects (Coolen, Dangles, & Casas, 2005), as well as in vertebrates such as fishes (Laland and Williams, 1998), birds (Barber & Kimbrough, 2015; Bednekoff & Balda, 1996; Dawson & Foss, 1965; Heinrich & Pepper, 1998) and mammals (Bandura, Ross, & Ross, 1961; Bunch & Zentall, 1980; Isbaine, Demolliens, Belmalih, Brovelli, & Boussaoud, 2015; Jurado-Parras, Gruart, & Delgado-García, 2012; Leggio et al., 2000; Meltzoff & Decety, 2003; Tomasello, Davis-Dasilva, Camak, & Bard, 1987; Yeater & Kuczaj, 2010). Since the pioneering work of Bandura et al. (1961) in humans, it has been shown that the ability to learn by observation is already present at birth and plays a crucial role in developing and mastering languages, social interactions or the use of various tools relevant to everyday life (Meltzoff & Decety, 2003; Nadel &

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* Correspondence: P. Meyrand, Institut des Maladies Neurodégénératives, CNRS UMR 5293, Université de Bordeaux, Bât B2 Allée Geoffroy St Hilaire CS50023, 33615 Pessac, France.
E-mail address: pierre.meyrand@u-bordeaux.fr (P. Meyrand).
[1] These authors share last authorship.

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Butterworth, 1999). More recently, some disorders such as the autism spectrum or dyslexia have been partly related to the inability to learn by observation (Foti et al., 2014; Menghini, Vicari, Mandolesi, & Petrosini, 2011).

Studies have shown that rodents are able to learn by observing a conspecific performing complex appetitive tasks such as pushing a joystick in a given direction (Heyes & Dawson, 1990; Heyes, Jaldow, & Dawson, 1994) or pressing a lever for a food reward (Will, Pallaud, Soczka, & Manikowski, 1974; Zentall & Levine, 1972). Similarly, information about aversive events can be acquired through social observation as shown by the adoption of crouching postures or immobility or discriminative avoidance in rats, *Rattus norvegicus* (Del Russo, 1975; Rice & Gainer, 1962) and freezing behaviour in mice, *Mus musculus* (Jeon et al., 2010) after observing distressed conspecifics receiving mild electric foot shocks.

Much less is known about spatial observational learning, as a subcategory of social learning, in rodents. As recently demonstrated, rats observing companion rats performing the hidden platform or cued platform versions of the Morris water maze can improve their performance when subsequently tested in the pool (Leggio et al., 2000, 2003). Interestingly, this observation-induced beneficial effect was interpreted by the authors predominantly as a procedural form of learning rather than as a pure localization form of learning since no evidence of restricted search towards the platform location could be clearly detected during task execution. Thus, the ‘knowing how’ component of the water maze learning procedure benefited more from observational learning than ‘knowing where’ or ‘knowing what’ components. Therefore, whether observation of a complex spatial task that includes learning multiple spatial locations may promote the formation of spatial cognitive maps and enable their successful use during testing has remained elusive. To address this issue, we developed a set of controlled appetitive behavioural procedures using an eight-arm radial maze in which the spatial position of specific baited arms in the maze learnt by demonstrators could be observed by rats watching the maze from an observational cage placed above it.

Another related question addressed in the present study concerned the incidence of mistakes made by demonstrators on the effectiveness of observational learning. It has been shown in cats, *Felis catus*, that observation of skilled performances is less beneficial than observation of the learning process itself (Herbert & Harsh, 1944). In humans and monkeys, learning by observation can recruit some neural circuits that specifically encode errors made by demonstrators (Monfardini et al., 2013; Yoshida, Saito, Iriki, & Isoda, 2012), suggesting that the monitoring of conspecifics' mistakes may play an important role in the process of learning by observation. These findings contrast with studies pointing to the importance of perfect demonstration (Zentall & Levine, 1972). We therefore compared the effect of observation of a trained demonstrator, providing nearly perfect information concerning the localization of baited arms, with the effect of observing the trial-and-error learning by an inexperienced demonstrator. In addition to examining the impact of information value (presence or absence of errors during observation) on the efficacy of observational learning, we also aimed to unravel the type of learning strategies (use of abstract procedural rules potentially efficacious regardless of the precise special position of the baited arms observed and/or of spatial cognitive maps specific to the location of baited arms) that were relevant for producing a beneficial effect of observation on spatial learning. To distinguish between the strategies, we deliberately exposed observer rats to a mismatch in the position of the baited arms in between observation and testing.

METHODS

Experimental Subjects

The data were collected from 132 adult male Long Evans rats (250–350 g) obtained from our regular supplier (Janvier Labs, Saint-Berthevin, France) and housed two per cage (480 × 265 mm and 210 mm high, Techniplast, Buguggiate, Italy) in a temperature- (22 ± 1 °C) and humidity-controlled (50 ± 10%) animal facility under an automatic 12 h light/dark cycle (lights on at 0700). Appropriate bedding (poplar wood granules, Lignocel Select Fine, Safe, Augy, France) was added to each cage and changed twice a week). Rats had ad libitum access to food and water for the first 10 days after their arrival and were then gradually food restricted to maintain their body weight at 85% of their ad libitum body weight throughout the experiments while access to water remained free. All procedures took place during the light cycle.

Apparatus

The apparatus was an elevated eight-arm radial maze purchased from IMETRONIC (Pessac, France). As illustrated in Fig. 1, it was composed of a central platform (40 cm in diameter) from which radiated eight identical arms (70 cm long and 15 cm wide). The entrance to each arm of the maze was controlled by automated sliding doors that could be controlled manually by an experimenter sitting in an adjacent room. To prevent rats from jumping from one arm to another or onto the floor, transparent partitions (16 cm long and 23 cm high) were attached on both sides of the proximate part of each arm whereas transparent body guards (3.5 cm high) were fixed along the more distal part of the arms. Each arm was terminated by a small platform with a small shaft (diameter 2 cm, depth 1 cm) in which food rewards were delivered. These rewards were small chips of crunchy chocolate rice (Kellogs' Chocopops). The observational cage consisted of a box (31 × 31 cm and 22 cm high) where all surfaces, except for the roof, were made of stainless-steel wire netting (open spaces of 1 by 1 cm). The cage was located 50 cm above the surface of the maze, equidistantly from the distal parts of two arms of the maze, with one of its side situated at 50 cm from the edge of the maze's central platform (Fig. 1). Four different configurations (124, 782, 146, 368) were used depending on the experiment (Table 1) with rats randomly allocated to one of these configurations. While baited arms were not equally distant from

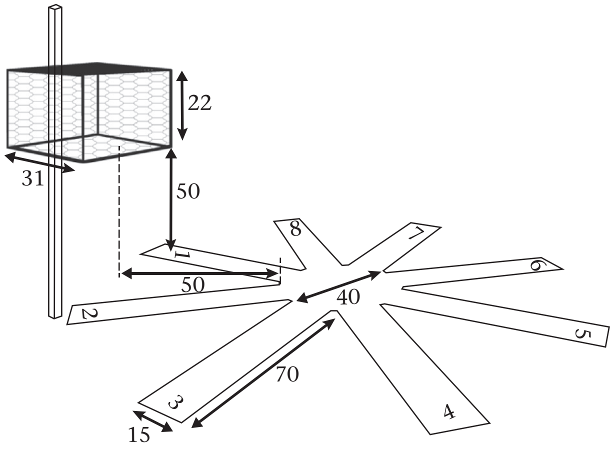

Figure 1. Schematic diagram of the experimental set-up used in the observational learning paradigm, showing the eight-arm maze with its arms labelled from 1 to 8 and the observer's cage as well as their dimensions and relative position (solid lines with arrows, cm).