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'Conformity' in Norway rats?

BENNETT G. GALEF & ELAIN E. WHISKIN Department of Psychology, Neuroscience & Behaviour, McMaster University

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In a recent paper, Whiten & van Schaik (2007, *Philosophical Transactions of the Royal Society of London, Series B*, **362**, 603–620) suggested that although a tendency to conform to the behaviour of others is widespread in animals, only chimpanzees and humans will ignore personally acquired knowledge of a superior behavioural alternative and copy the behaviour of others expressing a less effective behaviour. Here we show that 'observer' Norway rats, *Rattus norvegicus*, that have learned either that one food is toxic and another safe or that one food tastes good and another is less palatable will ignore their personal experience and choose to eat an unpalatable or presumably toxic food after interacting with 'demonstrator' rats that have eaten that food. Such observer rats will eat as much unpalatable or presumably toxic food after interacting with demonstrator rats that have eaten them as they would if they had no personal experience of superior alternatives. We discuss the similarity of rats' total reliance on socially acquired information when in possession of conflicting personal information to 'conformity' in chimpanzees and humans.

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In a recent paper, Whiten & van Schaik (2007) suggested that although a tendency to conform to the behaviour of others is widespread in animals (Day et al. 2001; Kendal et al. 2004), the motivation to copy others is particularly strong in chimpanzees and humans, and, in these species alone, supersedes use of personal knowledge. In the authors' words (Whiten & van Schaik 2007, page 611) 'What may be distinctive about the chimpanzee and human cases is that conformity overrides the discovery of valid alternative means', although Kendal et al.'s (2004) work with guppies, *Poecilia reticulata*, suggests that, at least under some circumstances, guppies 'conform' in Whiten & van Schaik's (2007) sense of the word.

The data supporting Whiten & van Schaik's (2007) assertion that chimpanzees conform are based on a study by Whiten et al. (2005) in which one member of each of two groups of chimpanzees was trained to either 'poke' or 'lift' to obtain food. The authors then examined acquisition and maintenance of the two methods by other group members that could acquire food by either poking

Correspondence: B. G. Galef, Jr, Department of Psychology, Neuroscience and Behaviour, McMaster University, Hamilton, ON L85 4K1, Canada (email: galef@mcmaster.ca). or lifting. The results of the study provided compelling evidence that socially acquired behaviours can be maintained in a chimpanzee population. The evidence of conformity was less clear. However, regardless of how the results of the Whiten et al. (2005) experiment are interpreted, the claim of Whiten & van Schaik (2007) that chimpanzees and humans are unique in their reliance on socially acquired information despite individually acquired contradictory information goes beyond these data, making a general case concerning the relative reliance on social and individual learning of chimpanzees, humans and members of other species. It is the reliability of this generalization that we address here.

In the Kendal et al. (2004) study of guppy feeding site selection mentioned above individual subjects were given a choice between two feeding patches, one behind an opaque barrier and the other in a location where they had previously seen a group of other guppies feeding. Even subjects that had previously fed behind the barrier chose the site where they had seen other guppies feeding, not the site where they had themselves fed. Possibly, in guppies, the motivation to join a school outweighs the motivation to go to a known source of food. If so, the observed conformity in guppies may be a quite different phenomenon from conformity in primates.

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Results of several previous experiments carried out in our laboratory suggest that, like the humans and chimpanzees to which Whiten & van Schaik (2007) call attention, Norway rats, *Rattus norvegicus*, might copy the behaviour of others even when their personal experience indicates that such conforming leads to inferior outcomes (Galef et al. 1983, 1990; Galef 1986). The present experiments were designed to test that possibility directly.

In previous experiments, we examined food choices in Norway rat 'observers' that, for example, ate a cinnamonflavoured food and were then injected with a toxin before they interacted with 'demonstrator' rats that had eaten cinnamon-flavoured food. When offered a choice between cinnamon-flavoured and cocoa-flavoured food, such observer rats ate more cinnamon-flavoured food than did subjects that were poisoned after eating cinnamon-flavoured food but not given an opportunity to interact with conspecific demonstrators that had eaten that food (Galef et al. 1983, 1990). Yoerg (1991) reported a similar result in spotted hyaena, *Crocuta crocuta*, and Nicol (2004) suggested that social learning about foods might also be important in overcoming unlearned aversions in chickens, *Gallus gallus spadiceus*.

In all of our previous experiments examining reliance on socially acquired information that contradicts rats' personal experience of foods, demonstrators interacted with observers before the observers had an opportunity to eat a food other than the one that they had been trained to associate with illness. Consequently, observers did not have personal experience of a valid alternative before they were subjected to social influence. It could, therefore, be argued that these earlier experiments did not provide evidence that rats conform, in the unique way that Whiten & van Schaik (2007) propose that chimpanzees and humans do. The present experiments were designed to overcome this deficiency and to test directly the hypothesis that in Norway rats, as in chimpanzees and humans, a tendency to copy the behaviour of others can completely override the tendency to engage in behaviours that personal experience indicates are superior to those in which others are engaged.

EXPERIMENT 1: CHOOSING BETWEEN TOXIC AND SAFE FOODS

In experiment 1, we first induced an aversion to cinnamon-flavoured food in rats, and then either gave them or did not give them a choice between cinnamon- and cocoaflavoured foods for 23 h before they interacted with demonstrators that had eaten cinnamon-flavoured food. We determined whether prior individual experience of the safe cocoa-flavoured food affected the intake of cinnamon-flavoured food by subjects offered a choice for 24 h between cinnamon- and cocoa-flavoured foods.

Methods

Subjects

Fifty-one 7- to 8-week-old female Long–Evans rats acquired from Charles River Canada (St Constant, Quebec,

Canada) served as subjects. After transportation from the supplier to our laboratory in Hamilton, Ontario, we housed subjects for 1 week in pairs in shoebox cages where they were maintained ad libitum on tap water and pellets of Teklad Rodent Diet 8640 (Teklad Mills, Madison, WI, U.S.A.). A further 68 9- to 10-week-old female Long–Evans rats that had served as subjects in previous experiments served as 'demonstrators'. We assigned 17 of the subjects to an experimental group and 17 to each of two control groups ('social' and 'individual-experience'; see Procedure).

Apparatus

During the experiment, all subjects resided in individual, wire-mesh hanging cages measuring $20 \times 20 \times 34$ cm. We presented food to subjects in semicircular, stainlesssteel food cups (10 cm in diameter and 5 cm deep).

Diets

We composed two diets by mixing either 10 g of ground cinnamon (McCormick Canada, London, ON: diet cin) or 20 g of cocoa (Hershey's Canada Inc., Mississauga, ON; diet coc) with sufficient powdered Teklad Rodent Chow 8640 (diet 8640) to make 1000 g of diet.

Procedure

We placed all demonstrators and subjects on a fooddeprivation schedule, feeding them diet 8640 for 1 h/day for 2 days. On the third day of scheduled feeding, we gave all subjects cinnamon diet for 1 h, and immediately afterwards injected each with 1.0% of their body weight isotonic (0.13 M) lithium-chloride solution. We then gave all subjects 23 h to recover from the effects of injection.

At the end of the 23 h recovery period (on day 1 of testing), we gave each subject that we had assigned to the experimental condition and each subject that we had assigned to the 'social-control' condition two weighed food cups: one cup contained diet cin and the other diet coc. Twenty-four hours later, we removed the food cups from the cages of these 34 subjects and determined the percentage of each subject's 24 h intake that was diet cin, the diet associated with illness. While the 34 subjects that we had assigned to experimental and social-control conditions had access to diets cin and coc, we provided subjects assigned to the 'individual-experience' control condition with a food cup containing unflavoured diet 8640.

While we weighed the food cups taken from observers' cages, we gave each demonstrator, for 1 h, a weighed food cup containing diet cin. At the end of the 1 h demonstrator-feeding period, we placed two demonstrators in succession, each for 30 min, in the home cage of each of the 34 subjects assigned to experimental and 'individual-experience control' conditions and allowed demonstrators and observers to interact freely. While subjects assigned to experimental and individual-experience control conditions interacted with demonstrators, subjects assigned to the social-control condition remained alone in their cages.

At the end of the 1 h period of interaction between demonstrators and observers, we removed demonstrators from the experiment, and (on day 2 of testing) offered each of the 51 subjects a choice for 24 h between two weighed food cups, one containing diet cin and the other diet coc. At the end of day 2 of testing, an experimenter weighed the food cups from each subject's cage and determined the percentage of each subject's total intake that was diet cin.

Ethical note

The McMaster University Animal Research Ethics Board approved the procedures used in both experiment 1 and experiment 2 (AUP 04-06-28 and AUP 07-06-35).

Results and Discussion

During the hour preceding injection with lithiumchloride solution, subjects ate 3.2-6.4 g of diet cin (mean ± 1 SE = 5.1 ± 0.3 g). During the hour preceding their interaction with observers, demonstrators ate 3.1-6.0 g of diet cin (4.6 + 0.2 g).

During testing on day 1, observers assigned to both experimental and social-control conditions showed a marked aversion to diet cin, the diet that had been associated with illness, indicating that they had learned an aversion to that diet (Fig. 1). They also ate substantial amounts of diet coc $(5.0-9.6 \text{ g}; \text{mean} \pm 1 \text{ SE} = 6.8 \pm 0.3 \text{ g})$, thus establishing personal knowledge of a valid alternative to ingesting diet cin.

A one-way ANOVA performed on the percentage of diet cin eaten by subjects assigned to experimental and control groups on day 2 of testing revealed a significant effect of group assignment on the percentage diet cin eaten by subjects ($F_{2,48} = 9.44$, P < 0.01; Fig. 1). Subsequent Tukey– Kramer multiple comparison post hoc tests revealed



Figure 1. Mean \pm SE percentage of diet cin eaten by experimental and control subjects on days 1 and 2 of experiment 1.

significant differences between the social-control group and both the experimental group and the individualexperience control group (social-control versus experimental group: q = 5.22, P < 0.01; individual-experience control versus social-control group: q = 4.419, P < 0.01), but no significant difference between the experimental and individual-experience control group (q = 0.81, P = 0.72). In summary, interaction with demonstrators fed diet cin had a profound effect on subjects' aversion to diet cin, and prior individual experience of the safe diet, diet coc, had no effect on subjects' subsequent reliance on socially acquired information when choosing between diet cin and diet coc. Norway rats showed conformity in Whiten & van Schaik's (2007) sense of the word.

EXPERIMENT 2: CHOOSING BETWEEN PALATABLE AND UNPALATABLE FOODS

In experiment 2, instead of using taste-toxicosis conditioning to teach subjects that cinnamon-flavoured diet was undesirable, as we had done in experiment 1, we increased the palatability of cinnamon-flavoured diet by adding substantial amounts of sugar to it. We then determined: (1) whether subjects that had learned that cinnamon-flavoured diet was preferable to cocoa-flavoured diet would increase their intake of cocoa-flavoured diet after interacting with conspecifics that had just eaten cocoa-flavoured diet, and (2) whether reliance on socially acquired information was affected by prior individual experience of the relative palatability of cinnamon- and cocoa-flavoured diets.

Methods

Subjects

Thirty Long-Evans rats with a history of acquisition and maintenance identical to those of subjects in experiment 1 and a further 20 demonstrators, with a history identical to that of demonstrators in experiment 1, participated in the present experiment. We assigned 10 of the subjects to an experimental condition and 10 to each of two control conditions ('social' and 'individualexperience' see Procedure).

Apparatus

The apparatus was that used in experiment 1.

Diets

In the present experiment, we used the diet coc and diet 8640 that we had used in experiment 1 as well as a 'sugarcinnamon' (diet s-cin) that we prepared by combining 100 g of granulated sugar with 900 g of diet cin.

Procedure

We maintained all subjects in hanging cages on ad libitum tap water and diet 8640 until the start of the experiment. To begin, we placed demonstrators on a feeding schedule, eating diet 8640 for 1 h/day for 2 consecutive days, and on the third day of scheduled feeding, gave demonstrators weighed samples of diet coc for 1 h, before we placed each demonstrator with an observer for 30 min.

On day 1 of testing, for 23 h, each of the 20 subjects assigned to experimental and social-control conditions received two weighed food cups, one containing diet coc and the other diet s-cin. Whilst subjects assigned to experimental and social-control conditions were eating diets s-cin and diet coc, we fed subjects assigned to the individual-experience control condition unflavoured diet 8640. We then allowed each of the 20 subjects assigned to the experimental and individual-experience control conditions to interact for 30 min with a demonstrator that had just eaten diet coc, while subjects assigned to the social-control condition remained alone in their cages. Last, we offered each subject a choice for 24 h (day 2 of testing) between two weighed food cups, one containing diet coc and the other diet s-cin. At the end of day 2 of testing, an experimenter determined the amount of diets eaten by all subjects and calculated the percentage of each subject's total intake that was diet s-cin.

Results and Discussion

During the hour preceding their interaction with subjects, demonstrators ate 3.2-6.2 g of diet coc (mean ± 1 SE = 4.2 ± 0.3 g).

During the 23 h of testing on day 1, subjects assigned to both social-control and experimental conditions showed a marked preference for diet s-cin (Fig. 2) and ate substantial amounts of it $(13.2-21.7 \text{ g}; 18.4 \pm 1.1 \text{ g})$, thus establishing personal knowledge that diet s-cin had greater palatability than diet coc.

A one-way ANOVA performed on the percentage of diet s-cin eaten by subjects assigned to experimental and



Figure 2. Mean \pm SE percentage of diet s-cin eaten by experimental and control subjects in experiment 2.

control groups on day 2 of testing revealed a significant effect of condition on the percentage of diet cin eaten ($F_{2,27} = 5.93$, P < 0.01; Fig. 2). Tukey–Kramer multiple comparison post hoc tests revealed significant differences between intake of diet s-cin by subjects assigned to the social-control condition and subjects assigned to both the experimental and individual-experience control conditions (social-control versus experimental: q = 4.04, P < 0.05; individual-experience control versus social-control group: q = 4.37, P < 0.05), but no significant difference in the intake of diet s-cin by subjects assigned to the experimental and individual-experience control versus social-control group: q = 4.37, P < 0.05), but no significant difference in the intake of diet s-cin by subjects assigned to the experimental and individual-experience control conditions (q = 0.33, P = 0.89).

As in experiment 1, (1) experience with demonstrators had a profound effect on subjects' diet preferences and (2) individual experience of the more valuable diet (in this case, diet s-cin) did not have a significant effect on subjects' subsequent reliance on socially acquired information when choosing between diets. Once again, Norway rats showed conformity.

GENERAL DISCUSSION

There is a growing list of behaviours once described as unique to humans and subsequently discovered to have functional analogues in the behaviour of various animals (e.g. teaching: ants: Franks & Richardson 2006; meerkats: Thornton & McAuliffe 2006; pied babblers: Raihani & Ridley 2008; culture: guppies: Laland & Hoppitt 2003; cowbirds: White et al. 2007; great apes: Whiten et al. 1999; van Schaik et al. 2003; tool making: crows: Hunt 1996; chimpanzees: McGrew 1992). The present data describing the behaviour of Norway rats, together with an earlier report of conformity in chimpanzees (Whiten et al. 2005), suggest that conformity can now be added to the list of behaviours seen in both humans and other animals.

Conformity is, however, a somewhat unusual instance of behaviour once thought to be unique to humans but subsequently found in animals in that both human conformity and rat conformity have been studied extensively under controlled conditions, permitting more detailed comparisons between 'conformity' in humans and another species than is usually possible in the case of animal analogues of human behaviours. Such comparison provides evidence of both similarities and differences in the expression of 'conformity' in humans and rats (Galef, in press).

In rats and humans, the greater the number of models and the greater their uniformity in behaviour, the more likely a naïve subject is to act in accord with the information that conspecifics provide (Asch 1952; Gerard et al. 1968; Tanford & Penrod 1984; Chou & Richerson 1992; Galef & Whiskin 1995). Furthermore, in both rats and humans, the greater the discrepancy between the information provided by models and a subject's own personal knowledge, the less likely the subject is to behave in accord with the socially acquired information (Asch 1952; Galef & Whiskin 1998). Other aspects of conformity, especially those depending either on rewards or punishments meted out by group members or on shared identification among group members (for review, see Kelman 1958), have not yet been found in nonhuman animals. Whether the behavioural mechanisms supporting the 'conformity' seen in Norway rats, chimpanzees and human beings are similar to one another is an open and an interesting question.

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