

Big brains are not enough: performance of three parrot species in the trap-tube paradigm

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Abstract The trap-tube task has become a benchmark test for investigating physical causality in vertebrates. In this task, subjects have to retrieve food out of a horizontal tube using a tool and avoiding a trap hole in the tube. Great apes and corvids succeeded in this task. Parrots with relative brain volumes comparable to those of corvids and primates also demonstrate high cognitive abilities. We therefore tested macaws, a cockatoo, and keas on the trap-tube paradigm. All nine parrots failed to solve the task. In a simplified task, trap tubes with a slot inserted along the top were offered. The slot allowed the birds to move the reward directly with their bills. All but one individual solved this task by lifting the food over the trap. However, the parrots failed again when they were prevented from lifting the reward, although they anticipated that food will be lost when moved into the trap. We do not think that the demanding use of an external object is the main reason for the parrots' failure. Moreover, we suppose these parrots fail to consider the trap's position in the beginning of a trial and

were not able to stop their behaviour and move the reward in the trap's opposite direction.

Keywords Comparative cognition · General intelligence · Behavioural inhibition · *Ara chloroptera* · *Cacatua sulphurea* · *Nestor notabilis*

Introduction

The question of why some animal species evolved higher cognitive abilities than others is still unsolved. It has been proposed that dealing with complex environments (whether social or physical) demands increasing neuronal substrate to cope with the increasing amount of information (Dunbar and Shultz 2007). It has also been reported that brain size correlates with innovation rate, learning speed, mechanical problem-solving, and tool use (Lefebvre and Bolhuis 2003). Yet, it is still a matter of dispute whether cognitive abilities are ultimately selected by specific socio-ecological demands and if so, whether they are restricted to specific adaptive specialisations.

The trap-tube task has become a widely used paradigm to test the understanding of causality in the physical domain. Subjects are offered a horizontal Perspex tube with a trap attached to its ventral side. In order to obtain a reward, which is put into the tube next to the trap, the subjects have to pull or push the reward with a stick. This paradigm was invented by Visalberghi and Limongelli (1994) to investigate how capuchin monkeys consider dynamic spatial relations between tool, food, and trap. Thereupon, it was adopted and used to test causal reasoning in different animal groups including apes (e.g. Mulcahy and Call 2006), humans (Horner and Whiten 2007; Silva et al. 2005), corvids (e.g. Seed et al. 2006), and woodpecker

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finches (Tebbich and Bshary 2004). All these studies showed a similar pattern of results; some, but not all, individuals learned to retrieve the reward from the correct side of the tube, and the test performances showed a strong dependency on the set-up of the task (reviewed in Emery and Clayton 2009). It has been suggested that the cognitive demands of tool use might mask the animals' performance on the trap tube. The reduction in the task's complexity by pre-inserting a rake in the tube (Tebbich et al. 2007) or by enabling the subject to reach the reward directly might facilitate the task as it has been shown recently by Seed and colleagues allowing chimpanzees to move the reward with their fingers (Seed et al. 2009).

Interestingly, some individuals of the large-brained corvids acquired functional knowledge about the task beyond simple associative learning (Seed et al. 2006; Taylor et al. 2009a, b).

Another vertebrate group well known for its primate-like relative brain size (Iwaniuk et al. 2005) and cognitive abilities in the social and non-social domain is the Psittaciformes order (Auersperg et al. 2009; Huber and Gajdon 2006; Pepperberg 2006; Wanker et al. 2005). The aim of our study was to investigate whether parrots are also able to solve the trap-tube paradigm. Although there are sporadic reports of tool use in parrots (Borsari and Ottoni 2005), they are not common tool users in the wild. We therefore used four different versions of the trap tube to enable three different parrot species to perform this task. In the first version, we used experimental set-ups similar to those used by

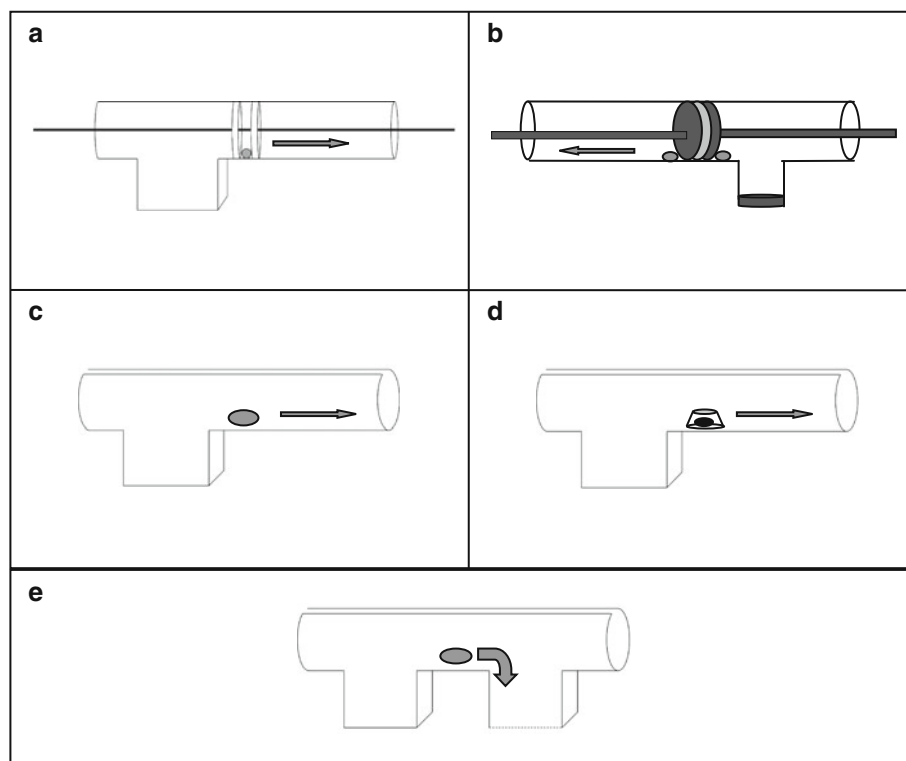
Tebbich et al. (2007) for rooks where a rake is pre-inserted into the tube. Parrots show skilful object manipulation and thus should fulfil the sensorimotor requirements of this task (Funk 2002). Additionally, in new versions of the trap tube, we reduced the complexity of the task by enabling the subjects to reach the reward directly with their bills via a slot along the upper part of the tube. We assumed that the parrots will learn to avoid the trap at least in the less complex slot tube.

Methods

This study is based on the independent work of two research groups. The six keas, *Nestor notabilis*, were tested in 2002/2003 in Vienna, Austria. The three macaws, *Ara chloroptera*, and the cockatoo, *Cacatua sulphurea*, were tested in 2008 in Hamburg, Germany. All tested birds were captive-reared and fully habituated to humans.

Tubes were made from transparent Perspex and had a trap next to its centre mounted at the ventral part (Fig. 1a). The birds had to rake the reward out to the correct side (i.e. without the trap). If they chose the side with the trap, the reward fell out of reach. In the trap tube presented to the keas, two sticks were pre-inserted, each with a disc attached to its end (Fig. 1b). The trap tube presented to the macaws and the cockatoo contained just one rake that could be pulled out of the tube on both sides. At its middle part, two transparent discs were attached, and in between them, the

Fig. 1 Test apparatuses. In order to obtain the reward, an individual must move it out of a Perspex tube with a trap attached to its *bottom*. The birds can push or pull one rake in (a) or pull one of two rakes in (b). In the slot tubes (c–e), a gap along its upper side enabled the parrots to move the reward directly with their bills. In (e) a second, non-functional trap without a *bottom* was added. Arrows indicate the direction of correct response



reward was placed (Fig. 1a). The slot tubes (Fig. 1c–e) had a gap (1.5 cm wide) along the upper side through which the parrots could move the reward directly with the bill. Therefore, no use of external objects was required in this task.

Six keas were tested first with the trap tube (Fig. 1b) and afterwards with the slot tube (Fig. 1c, d). Film containers or walnut shells baited with butter were used as a reward. In the control test with the slot tube, a transparent reward container was used, which was smooth and flat shaped, so the birds could not lift it (Fig. 1d).

Two macaws and the cockatoo were first tested with the slot tube (Fig. 1c). The two successful birds were tested on a second slot tube with two traps: one was functional and the other was non-functional with no bottom (Fig. 1e). Walnut shells were filled with parrot pellets (which are not included in their normal food dishes) as a reward. Afterwards, these two individuals and one additional macaw were tested with the original trap tube (Fig. 1a).

All individuals were tested in visual isolation from each other. Each task was presented in blocks of ten trials. The orientation of the tube was randomly determined and counterbalanced. The trial was stopped after the subject had pulled one rake. Keas were offered ten blocks of trap-tube trials, 20 blocks of slot tube, and 14 of slot-tube control. The macaws and cockatoo were given between 13 and 20 blocks of trials with the trap tube and as many blocks of trials with the slot tubes until they had reached the criterion of success. The criterion for a task being solved was set to 80% correct trials (gaining the reward) in each of two consecutive test blocks (16 correct out of 20 trials; binomial test, $P = 0.012$). Individual's side biases were tested per task using G test.

Results

When tested with the trap tube (for an example, see the online resource ESM_1.mpg), only one parrot solved the problem (see Table 1). This kea, Mismo, reached the learning criterion in block 4, but fell back to chance level afterwards.

In the slot-tube task, however, all parrots except one macaw succeeded, though they did not avoid the side with the trap. They solved the task in 8.5 test blocks on average (Table 1) mostly by subverting the task design (Fig. 2). The cockatoo raked the reward out of the trap with his foot (as shown in the online resource ESM_2.mpg). All other parrots started to lift the reward over the trap with their bill. The keas Bigo and Mismo were exceptions (Table 1). Bigo solved the slot tube in 18 out of the 20 trials of the first two test blocks by avoiding the side of the trap. However, in session 3, he lost the reward in half of the trials by moving it into the trap. In this session, he also lifted the reward

2 times over the trap and started to use this solution reliably during the next sessions to solve the task. Kea Mismo successfully retrieved the food in all ten trials of the first session by moving it to the side where there was no trap. But in the next five sessions, he often lost the reward in the trap and only rarely lifted the reward over the trap.

The performance did not exceed chance level in the control task that prevented the keas from lifting the reward. Also, the two parrots tested with the two-trap slot tube (trap control) chose the sides with the different traps equally often. They continued to lift the tube over the non-functional trap (Table 1, for an example, see the online resource ESM_3.mpg), although the reward had fallen through there in a few trials.

Although the subjects could move freely around the devices, the birds often had or developed a side bias during the different tasks. Furthermore, the behaviour of the birds was goal-directed and did not show much variation.

Discussion

In this study, we tested the problem-solving abilities of three different parrot species in four trap-tube versions. In the original trap-tube task that required the usage of a rake, no parrot solved the task reliably. In contrast, in apes and corvids (including even non-tool-using rooks), several individuals learned to solve this initial task in fewer trials (seventy or forty in rooks; Seed et al. 2006) than the parrots were offered in this study. Even one woodpecker finch (a natural tool user) solved the task with a tool apparently by “a rapid process of trial and error learning” (Tebich and Bshary 2004).

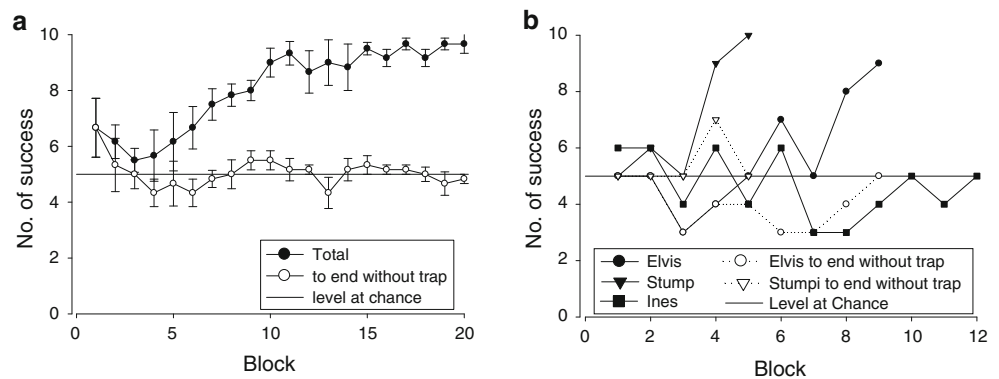
In the slot-tube version in which the subjects could directly move the reward with the bill or the foot, all parrots except one macaw solved the problem. However, they did not avoid the trap according to the spatial configuration of the reward and the trap in the beginning of the trial. Rather, they showed a local avoidance of the trap: in the cases where the reward was moved close to the trap, they developed the solution of lifting the food across the trap. The keas Bigo and Mismo were exceptions in that they applied the solution of spatial configuration right in the beginning of testing the slot-tube task. It can be argued that Bigo's decrease in performance after the beginning was because he started to elaborate the alternative and more intuitive local trap avoidance of lifting the reward. However, this explanation is unlikely to hold for Mismo that performed at chance level after session 1 without improving the local trap avoidance for another four sessions at least (Table 1). Also, the keas did not manage to retrieve the reward reliably at the side of the tube where there was no trap to cross when they were prevented from lifting the reward in the control task.

Table 1 Number of trials in which the different individuals retrieved a reward successfully in the different tasks

Task	Individual	Number of <i>test block</i> , data, and criteria performance										
Trap tube		<i>1</i>	<i>2</i>	<i>3</i>	<i>4</i>	<i>5</i>	<i>6</i>	<i>7</i>	<i>8</i>	<i>9</i>	<i>10</i>	
	Bigo (N.n.)	6	6	5	2	2nc	2	5	5	4	8	
	Bruce (N.n.)	7	4	6	5	7	5	5	5	5	5	
	John (N.n.)	3	4	6	7	2	4	5	4	5	4	
	Knut (N.n.)	5	3	8	6	7	4	7	6	5	8	
	Mismo(N.n.)	2	6	8	8pc	6	5	8	7	6	3	
	Tiffany (N.n.)	7	4	5	6	2	6	5	5	5	5	
	Elvis (C.s.)	4	5	5	5	5	5	5	4	7	5	
	Stumpi(A.c.)	3	2	5	5	5	7	4	5	6	6	
	Oli (A.c.)	5	3	3	4	3	4	5	5	5	5	
			<i>11</i>	<i>12</i>	<i>13</i>	<i>14</i>	<i>15</i>	<i>16</i>	<i>17</i>	<i>18</i>	<i>19</i>	<i>20</i>
	Elvis (C.s.)	7	4	4	8	4	5	5	4	5	–	
	Stumpi(A.c.)	2	4	4	3	6	5	4	4	4	6	
	Oli (A.c.)	5	5	4	–	–	–	–	–	–	–	
Slot tube		<i>1</i>	<i>2</i>	<i>3</i>	<i>4</i>	<i>5</i>	<i>6</i>	<i>7</i>	<i>8</i>	<i>9</i>	<i>10</i>	
	Bigo (N.n.)	9 (0)	9pc (0)	5 (2)	8 (3)	10 (5)	9 (4)	8 (4)	9 (4)	8 (3)	10 (5)	
	Bruce (N.n.)	3 (0)	5 (0)	6 (0)	2 (0)	2nc (1)	5 (1)	7 (2)	7 (3)	7 (2)	8 (1)	
	John (N.n.)	6 (0)	6 (0)	4 (0)	5 (1)	6 (1)	7 (2)	8 (3)	9pc (3)	9 (3)	10 (5)	
	Knut (N.n.)	5 (0)	5 (1)	5 (0)	5 (0)	6 (1)	4 (1)	5 (0)	7 (1)	7 (0)	7 (2)	
	Mismo(N.n.)	10 (0)	6 (0)	6 (0)	6 (1)	6 (1)	7 (1)	8 (4)	8pc (2)	8 (3)	10 (5)	
	Tiffany (N.n.)	7 (0)	6 (4)	7 (1)	8 (3)	7 (0)	8 (5)	9pc (3)	7 (4)	9 (4)	9 (3)	
	Elvis (C.s.)	5 (0)	5 (0)	3 (0)	4 (0)	5 (1)	7 (4)	5 (2)	8 (4)	9pc (4)	–	
	Stumpi(A.c.)	5 (0)	6 (1)	5 (0)	9 (2)	10pc (5)	–	–	–	–	–	
	Ines (A.c.)	6 (0)	6 (0)	4 (0)	6 (0)	4 (0)	6 (0)	3 (0)	3 (0)	4 (0)	5 (0)	
			<i>11</i>	<i>12</i>	<i>13</i>	<i>14</i>	<i>15</i>	<i>16</i>	<i>17</i>	<i>18</i>	<i>19</i>	<i>20</i>
	Bigo (N.n.)	10 (5)	10 (5)	10 (5)	10 (5)	9 (3)	10 (5)	10 (5)	9 (4)	10 (5)	10 (5)	
	Bruce (N.n.)	8pc (1)	9 (4)	9 (5)	10 (3)	10 (4)	9 (4)	9 (3)	10 (6)	9 (6)	10 (5)	
	John (N.n.)	10 (6)	10 (5)	10 (4)	10 (5)	10 (5)	9 (4)	10 (5)	9 (4)	10 (6)	8 (3)	
Knut (N.n.)	8 (3)	5 (0)	5 (3)	8 (4)	9pc (4)	10 (5)	10 (5)	9 (4)	9 (4)	10 (5)		
Mismo(N.n.)	10 (5)	9 (4)	10 (6)	5 (5)	9 (5)	8 (3)	9 (4)	10 (4)	10 (5)	10 (5)		
Tiffany (N.n.)	10 (5)	9 (3)	10 (5)	10 (5)	10 (4)	9 (3)	10 (5)	8 (3)	10 (4)	10 (6)		
Ines (A.c.)	4 (0)	5 (0)	–	–	–	–	–	–	–	–		
Slot tube; lift control		<i>1</i>	<i>2</i>	<i>3</i>	<i>4</i>	<i>5</i>	<i>6</i>	<i>7</i>	<i>8</i>	<i>9</i>	<i>10</i>	
	Bigo (N.n.)	5	6	5	5	8	6	2	4	6	4	
	Bruce (N.n.)	1	5	5	5	5	7	5	4	5	5	
	John (N.n.)	2	6	6	6	6	6	5	5	7	5	
	Knut (N.n.)	4	5	5	5	3	5	5	5	3	5	
	Mismo(N.n.)	5	5	5	5	3	5	5	5	2	4	
	Tiffany (N.n.)	4	5	6	4	6	5	5	6	5	5	
			<i>11</i>	<i>12</i>	<i>13</i>	<i>14</i>						
	Bigo (N.n.)	6	3	5	6							
	Bruce (N.n.)	3	5	6	7							
Slot tube; trap control		<i>1</i>	<i>2</i>	<i>3</i>	<i>4</i>							
	Elvis (C.s.)	8 (3)	6 (4)	9 (3)	9pc (7)							
	Stumpi (A.c.)	8 (5)	8pc (6)	–	–							

Results are grouped for blocks of ten test trials
pc (positive criterion): reward retrieved successfully for the first time in 80% of the trials in each of two consecutive test blocks with ten trials each, *nc* (negative criterion): 80% failure in two consecutive test blocks. Data of test blocks are in **bold** if success reached significance according to 2-sided binomial testing (9 or 1 successes out of 10 trials yields $P = 0.021$). N.n.: *Nestor notabilis*; A.c.: *Ara chloroptera*; C.s.: *Cacatua sulphurea*. Slot tube: Data in brackets indicate the number of trials when food was lifted over the trap hole

Fig. 2 Performance of the parrots on the slot tube they were offered first. The y-axis gives the number of successful trials per block. One block includes 10 trials. **a** Mean performance ($x \pm SD$) of six keas. **b** Individual performance of macaws Stumpi and Ines and cockatoo Elvis



Hrubesch et al. (2009) found that chimps did not switch to an alternative solution once their first solution started to fail. But contrary to Hrubesch et al.'s testing situation, the keas experienced an alternative behaviour as rewarding in about half of the trials but still did not consolidate it as the novel solution.

The side preference might explain the initial side choice of an individual, but the question remains why the animals could not react accordingly to the device's arrangement (e.g. inhibit the side preference when necessary and chose the other non-preferred direction).

Thus, the most interesting part of the results is that a few individuals might successfully avoid the trap by considering the spatial configuration of a simplified task. But this performance, in contrast to simpler solutions, holds only in the short term and is not stable. This parallels the findings in naturally non-tool-using rooks where the only individual that mastered a trap-tube transfer task of spatial configuration (Seed et al. 2006) later completely failed in further transfer tasks (Tebbich et al. 2007).

Although the overall picture in transfer tasks of the trap-tube paradigm may not be very convincing in rooks (Tebbich et al. 2007), several individual rooks did reliably better in the initial trap-tube task than any of our parrots did. There are several species differences that might explain why parrots, despite their large brains and sophisticated sensorimotor skills, performed less well. It is possible that the parrots were less likely than corvids to pursue the movement of the reward in the trap when pulling the rake. As food-storing birds, corvids may be more likely to do so because they put items into holes and cover them with objects. This behaviour most likely is controlled by visual feedback provided by the food item in the cache hole (Bugnyar et al. 2007).

A comparison of the brain's structure of these two avian groups might give hints for further explanations: parrots and corvids have similar relative big brain sizes. These "big brains" mainly derive from an extraordinary enlargement of pallial associative areas of the telencephalon (the mesopallium and nidopallium). This, together with the striatopallidal areas, separates the psittaciformes and passerine from most

of the other avian groups (Iwaniuk and Hurd 2005). Furthermore, non-telencephalic brain structures are enlarged such as the cerebellum, which is thought to be involved in motor control and learning (Iwaniuk et al. 2009). This "enlargement" is not the consequence of relative growth of the total size but rather due to a surface foliation which increases the neural processing capacity (Iwaniuk et al. 2009). Sultan (2005) indicated "...that the cerebellum in large-brained birds does not scale uniformly, but occurs in two designs. Crows, parrots and woodpeckers show an enlargement of the cerebellar trigeminal and visual parts..." and suggested that "...this may be related to their repertoire of visually guided goal-directed beak behaviour". Besides these similarities, parrots and corvids may differ in other brain areas and/or on a finer neuronal level. Both groups are vocal learners, and their vocal pathways are embedded within brain areas that are active during limb and body movements (Jarvis 2007). This makes it likely that vocal learning is connected to motor control. The fact that the vocal pathways of parrots and corvids differ in their connectivity (Jarvis 2007) and their precise location (the parrot posterior regions are more anterior and laterally than the corresponding areas in other vocal learners) (Feenders et al. 2008) might lead to speculation of some differences in the underlying neural tissue for other behaviours than vocalisation. It is also important to bear in mind that the mesopallium and the nidopallium as higher order associative brain structures get input from multiple sources. Thus, their enlargement might derive from different demands for neuronal processing capacity. Mehlhorn et al. (2010), for example, showed that the New Caledonian crows (*Corvus moneduloides*) have a relative large mesopallium, even in comparison to the Carrion crows (*Corvus corone corone*) and suggested that this might stem from the cognitive demands of tool use.

Nevertheless, it is far from clear whether differences in neuronal structure of parrots and corvids are responsible for their behavioural differences concerning the trap-tube paradigm. More detailed analyses of the precise neuronal organisation and its influence on behaviour are needed before further conclusions can be drawn.

We suggest that other more general behavioural control mechanisms might play a crucial role in solving this paradigm. The good performance of corvids might be caused by their inhibitory control. As Taylor et al. (2009a) mentioned, the three successful crows in their study could repeatedly inhibit their initial behaviour and switched the sides of the tube within one trial to gain the reward. Thus, it was assumed that they understood something about the spatial configurations of the task. The unsuccessful subjects never did inhibit their initial behaviour. Similarly, we observed only very few trials in which the parrots switched sides within one trial (six out of 3,300 trials). This indicates that corvids might have less difficulty in inhibiting behaviour in respect of a larger area around a reward, at least when it is out of reach. Yet, we still lack directly comparative investigations about inhibitory competence of these species. Again, such a competence can be regarded as adaptive in corvids for making food caches and pilfering others in a social setting that demands inhibition (Bugnyar et al. 2007).

In summary, our results show that although the parrots recognised the possible loss of the reward at the trap and created counter strategies, these large-brained subjects failed, with few non-reliable exceptions, to move the reward to the appropriate direction in the tube even when the demanding need to use an interfering rake was removed. This is true even though the one-trap-tube paradigm could be solved with simple associative rules (Silva et al. 2005). This provides an example of the limits in domain general intelligence. However, we see these limits in more general control mechanisms of behaviour, such as inhibition, that may play a minor role in object manipulation by nut cracking or root digging parrots (Clarke 1970) where motor acts are likely to be self-rewarding.

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Ethical standards The presented experiments comply with the current laws of the countries in which they were performed.

Conflict of interest Herewith we declare that the authors do not have any conflict of interest.

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