

Induction of Strategies and Habits in Rats Through two Behavioural T-maze Paradigms

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Summary

Two different behavioural paradigms in T-maze were developed with the aim to induce patterns of behavioural persistence in rats. These new procedures were based not on traditional asymmetric reinforcement methodology, but on a modified Krechevsky paradigm using olfactory stimuli, where we found rats spontaneously developed patterns of behavioural persistence – or behavioural “strategies” - with less than 1% probability of these occurring by chance. Rats predominantly developed spatial position (win-stay) strategies, but also spatial alternation (win-shift) strategies, olfactory strategies, and, to a minor degree, olfactory alternation strategies. Spatial alternation behaviour was significantly more frequent during early (first 40 trials) than during late testing. Position bias (spatial win-stay behaviour) increased gradually with the number of trials and was significantly increased in late (over 120 trials) compared to early testing. In the second paradigm, habits were induced in rats using a forced-choice procedure. After 100 forced-choice trials of running to the same side in a T- or Y-maze, the rats showed a significant propensity for this side when allowed to choose freely, compared to the situation in which only one forced-choice trial had been performed. Ten forced trials were not sufficient to induce this habit. Both paradigms may be useful for modelling aspects of human habit formation and for behavioural neuroscience experiments.

Introduction

Two behavioural tendencies compete in animals; the tendency to persist in a present behaviour and the tendency to change or shift behaviour. In foraging behaviour, win-stay as well as win-shift strategies occur, and different species appear to prefer one over the other of these strategies (*MacDonald et al., 1994*). Behavioural shifting paradigms in the laboratory, e.g. attentional set-shifting (*Roberts et al., 1988*), have been intensively studied in animals during the last two decades, and neural substrates of various kinds of shifts have been suggested (*Robbins, 2007*). Behavioural persistence, e.g. habit

formation, has often been studied in laboratory animals by means of responses learned or overlearned by the traditional asymmetric reinforcement method (*Graybiel, 2008*). Behavioural shifting paradigms as well as persistence paradigms performed in laboratory animals are possibly relevant models for studies of aspects of human pathological behavioural inflexibility as for instance seen in OCD (obsessive compulsive disorder) (*Clarke et al., 2005; Yadin et al., 1991*). The purpose of the present study was to develop and validate the usefulness of two novel behavioural paradigms for modelling behavioural persistence and habit formation in the rat. Neither of the paradigms is based on learning by asymmetric reinforcement. They may thus prove useful and assist in the acquisition of a more complete picture of the neural substrate of behavioural persistence and may also be of potential relevance for modelling aspects of human OCD.

In the first paradigm rats were allowed for a large

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number of trials to choose freely between the right and left arm of a T-maze. Each arm contained one of two different olfactory stimuli, and the rats were rewarded for all responses. This paradigm was a novel T-maze variant of Krechevsky's classic paradigm (Krechevsky, 1932). Krechevsky was one of the early cognitive theorists within the animal learning field. He demonstrated that rats do not - as behaviourists claimed - perform random choices in mazes in the so-called "pre-learning phase", but exhibit highly structured choice behaviour. Krechevsky took his findings as evidence for systematic testing of problem-solving strategies - or "hypotheses" in the terminology of Krechevsky - in rats, a marked cognitive position. In the present modified Krechevsky paradigm, we tested the hypothesis that rats would spontaneously develop patterns of behavioural persistence - or behavioural "strategies" - in this paradigm, rather than exhibit random behaviour. We are primarily focusing upon the paradigm as a possible model for some forms of human behavioural persistence.

The otherwise important discussion, whether the behavioural structuring seen in the paradigm is best described in a cognitive or operant theoretical framework, is brought up in the Discussion, but is not the primary subject of the present study. We use the cognitive term "behavioural strategies" - although not "problem-solving strategies" (see Discussion) - for the structured behaviour occurring in the Krechevsky paradigm, because we find it most likely that the behavioural structuring is initiated from within the animals as a result of cognitive processes, although other explanations are possible (see Discussion).

In the second paradigm, a forced-choice procedure, we attempted to induce pre-defined spatial habits in rats in T- or Y-maze. The hypothesis was that rats trained by a forced-choice procedure would continue to respond according to a forced habit when subsequently allowed to choose their responses freely. Two different types of maze were used in order to examine the effect of the type of maze.

Animals

A total of 23 male experimentally naïve Wistar rats (Charles River Labs., Sulzfeld, Germany), weighing 250 g at the start of the experiment, were used. Female rats were not included in the study to avoid confounding variables associated with oestrus cycle variation. Nine rats were used in the Krechevsky paradigm, eight rats were used in the forced-choice procedure in the T-maze, and six rats were used in the forced-choice procedure in the Y-maze. The rats were housed singly in Macrolone Type III cages (Scanbur, Køge, Denmark) with aspen bedding (Tapvei Estonia, Harjumaa, Estonia) in a temperature (21 °C +/- 1 °C) and humidity (45-65%)-controlled environment and maintained at a 12 h/12 h light/dark cycle. Testing was conducted during the light phase. Daily food intake of Altromin 1314 (Altromin GmbH, Lage, Germany) was restricted and rats were maintained on 90 % of their free-feeding weight. Acidified (citric acid) tap water was available *ad libitum*. The experiments were in compliance with the European Communities Council directive 86/609/EEC and the recently revised Appendix A to the Council of Europe Convention ETS 123.

Mazes and olfactory stimuli

The T-maze was a beige-coloured Plexiglas maze (width: 10 cm; height: 20.5 cm; length of start alley: 38 cm; length of response arms: 30.5 cm) without a start box. In the modified Krechevsky paradigm only, flaps and odour bars were inserted into the maze arms. Three cm into each of the response arms a vertical flap was placed covering the width of the arm. The rats had to run through the flap in order to gain access to food. Each flap was made of plastic coated white paper and suspended from a horizontal string. The odour bars were made of a hollow plastic bar (length: 10 cm; width: 1.5 cm; height: 1.5 cm) perforated with small holes on the top side. A piece of felt, containing a few drops of herbal oil (Urtegaarden, Allingaabro, Denmark), was placed inside the plastic bar. One bar contained oregano oil (*Origanum vulgare*) and the other anis oil (*Pimpinella anisum*). The odour bars were placed on the

maze floor directly in front of the flaps of the response arms, one bar in each arm. The Y-maze was an off-white painted wooden maze (length: 80 cm; total width: 40 cm; width of response arms: 18 cm; height: 25 cm). The response arms were parallel and pointed directly forward. The maze had a start box with a transparent Plexiglas door. Both mazes were placed in a dimly lit room without ceiling lights. Light sources were placed symmetrically around the mazes.

Modified Krechevsky paradigm

Habituation

All rats were initially subjected to one 30 min habituation session in the T-maze on each of three consecutive days. During habituation mashed food was present at the end of both response arms, and the rats were allowed to explore and eat freely. Flaps - but no odour bars - were present in the maze. The experimenter was located by the end of the start alley of the maze.

Testing

The modified Krechevsky paradigm was carried out in the T-maze with odour bars inserted. The procedure was a novel version of a procedure first described by Krechevsky (1932). All rats were given 10 testing sessions. All testing sessions consisted of 20 trials, except for the first two sessions, that consisted of 10 trials. On each trial, one odour bar containing anis oil and one containing oregano oil were placed in the arms of the maze. The olfactory stimuli were randomised between right and left following a pseudo-randomisation. A given odour was placed equally frequently in the right and left arm of the maze, and a given odour was never placed in the same arm for more than three trials in a row. During trials the rats were released in the start alley of the maze and allowed to run through a flap into an arm of their own free choice. After a short eating period, aimed at 6 s for both right and left, the rats were picked up by the experimenter and placed in a small transport cage. Arm entries counted if the rats passed the flap line with both front paws. Inter-

trial intervals were approximately 15 s including the eating period. The experimenter was blind to the hypotheses of the study.

Data and data analysis

For each individual rat, the data for each session consisted of the sequence of responses made in the maze. It was noted for each response if it was to the right or left, and in addition the associated odour (anis or oregano) was recorded. "Strategies" were defined as response sequences consisting of at least six consecutive responses (less than 5 % probability of occurring by chance – see below) for the following types of responses: responses to the right only or the left only (position strategies), responses to anis only or oregano only (olfactory strategies), right-left alternation (spatial alternation strategies), and anis-oregano alternation (olfactory alternation strategies). The probability of response sequences was calculated using an approximation in which the response sequences were treated as separate, the response choices were treated as independent events, and the probability of responses to the right or left, anis or oregano were treated as equal (symmetric probability). The equation used was $P(A \text{ and } B) = P(A) P(B)$, in which $P(A \text{ and } B)$ is the probability of the events A and B occurring in sequence, and $P(A)$ and $P(B)$ are the probabilities of A and B occurring separately. The probability of each event (right, left, anis, oregano) occurring separately was $\frac{1}{2}$, and for a series of responses to the right only, the left only, anis only or oregano only, the probability of a particular sequences occurring was therefore calculated as $1/2^n$, n being the number of trials in the sequence. For alternation series – whether these were spatial or olfactory – this probability was multiplied by two, since alternation series could start by either of the two response possibilities. Thus, the approximate probability was below 5 % for all the considered types of 6-trial sequences (1.56 % for position and olfactory sequences; 3.12 % for alternation sequences), and below 1 % for all the considered types of 8-trial response sequences (0.39 % for position and olfactory sequences; 0.78 % for al-

termination sequences). For all strategies it was noted whether the response sequence was also in accordance with another type of strategy of at least the same length.

In addition, the following parameters were calculated for each session for each rat: the percentage of responding to the maze side preferred by the rat in that particular session (position bias), the percentage of responding to the odour preferred by the rat in that particular session (odour bias), the percentage right-left alternation, and the percentage odour alternation. For these parameters, all sessions (1 – 10) were compared by one-way ANOVA ($p < .05$ significance level), and only if any significant difference between sessions was revealed, was the last session (session 10) compared to each of the rest of the sessions using Bonferroni's Multiple Comparison Test ($p < .05$ significance level).

Forced-choice procedure

Habituation

Prior to testing, each rat was given one 30 min habituation session in the relevant maze (T- or Y-maze) on each of three consecutive days. During habituation mashed food was present by the end of each response arm, and the rats were allowed to explore and eat freely. No blocks restricting access to the arms were inserted into the maze. The experimenter was located by the start alley of the maze.

Testing

Similar forced-choice procedures were carried out in T- and Y-mazes in two separate experiments. During the forced-choice procedure, mashed food was present by the end of both response arms of the maze. On all trials rats were released in the start alley and allowed to run to the food and eat for a period aimed at 6 s for both right and left. On most trials one of the response arms was blocked by a block inserted into the maze. The block was a cardboard box of the same colour as the maze. The box had the same height as the maze and nearly the same width as the response alley. Smell from the food could pass at both sides. For each individual rat the blocked arm

was always the same (right or left), but the position of the blocked arm was randomised between rats. On the first session, the rats received one trial with one of the maze arms blocked. Thereafter, the block was removed and the rats were given 10 trials in which they could choose freely between arms (the 1-trial challenge). On session two, the block was inserted into the maze again in the same arm as before, and rats received 10 forced trials. The block was then removed, and rats were given 10 free-choice trials (the 10-trial challenge). Subsequently, the rats were subjected to 90 more forced trials spread over five sessions with the block inserted into the usual arm. On the last session, 10 more trials were given with the block inserted followed by 10 block-free trials (the 100-trial challenge). Arm entries counted if the rats entered the maze arm with all four paws. The experimenter was blind to the hypotheses of the study.

Data and data analysis

The sequence of right-left choices of the 10 free challenge trials was noted for each rat for the 1-trial, the 10-trial, and the 100-trial challenge. The percentage responding to the newly opened, previously blocked, side was calculated for each rat for the first five as well as the 10 trials of the 1-trial, the 10-trial, and the 100-trial challenge. The responses on the first five trials of the challenges were analysed as a measure of the immediate effect of the forced-trial procedure. The results of the three challenges were compared by one-way ANOVA ($p < .05$ significance level), and only if any significant difference between the challenges was revealed were the results of the three challenges compared individually using Bonferroni's Multiple Comparison Test ($p < .05$ significance level).

Results

Modified Krechevsky paradigm

Response sequences consisting of eight or more consecutive responses according to the same behavioural pattern or "strategy" (less than 1 % probability of occurring by chance) were found for all the

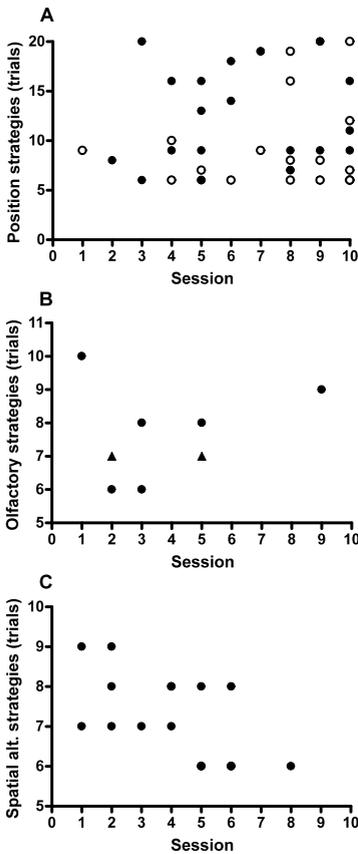


Figure 1. Spontaneous strategies occurring during the 10 sessions of the modified Krechevsky paradigm (n = 9). The number of responses (trials) in un-broken sequence performed in accordance with three different types of strategies is shown. Only strategies performed for at least six consecutive trials are shown. *A. Position strategies.* Filled circle: position strategies to the right. Open circle: position strategies to the left. *B. Olfactory strategies.* Filled circles and triangles: olfactory strategies towards anis. Open circles: olfactory strategies towards organo. Triangles: sequences that are in accordance with olfactory strategies as well as spatial alternation strategies. *C. Spatial alternation strategies.* For none of the position or spatial alternation strategies, was the full sequence also in accordance with an olfactory or olfactory alternation strategy.

response categories investigated: position responses (Fig. 1A), olfactory responses (Fig. 1B), spatial alternation (Fig. 1C), and olfactory alternation (not shown). However, for olfactory alternation, only one 8-trial sequence was found. The majority of the olfactory alternation strategies (six 6-trial sequences and four 7-trial sequences) occurred during position strategies of longer duration. However, two 6-trial sequences, five 7-trial sequences, and the 8-trial olfactory alternation sequence occurred at times when the rats did not exhibit any of the other behavioural strategies.

Strategies consisting of more than 10 consecutive responses were found only for position strategies, for which they were quite frequent (Fig. 1A). For individual rats the development in the response pattern was analysed over all 10 sessions to examine if response patterns could be found resembling the patterns that Krechevsky took as evidence for “hypotheses” in rats (see Discussion). The clearest example of such a behavioural pattern in a single rat is shown in Fig. 2. For the whole-session parameters (session 1-10) ANOVA revealed significant

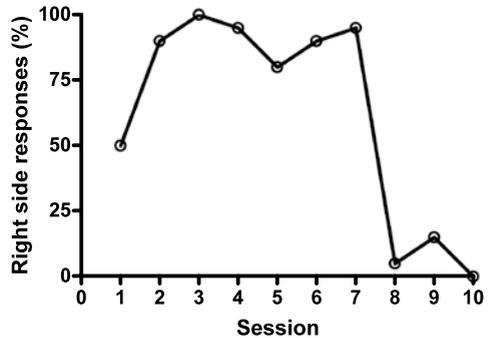


Figure 2. Behaviour of a selected rat from the present modified Krechevsky paradigm. Reproduction of a kind of behavioural pattern that Krechevsky – probably falsely – took as evidence for the existence of problem-solving “hypotheses” in rats. The percentage responses to the right is shown. On session one, the rat exhibited spatial alternation on 89% of the trials.

differences between sessions only for position bias ($F(9,80)=3.06, p<.01$) and spatial alternation ($F(9,80)=3.65, p<.001$). There was significantly less position bias on sessions 1 and 2 compared to session 10 (Bonferroni's Multiple Comparison Test, $p<.01$ for session 1; $p<.05$ for sessions 2) (Fig. 3A). There were significantly more spatial alternations on each of the sessions 1-3 compared to session 10 (Bonferroni's Multiple Comparison Test, $p<.001$ for session 2; $p<.01$ for sessions 1; $p<.05$ for session 3) (Fig. 3B).

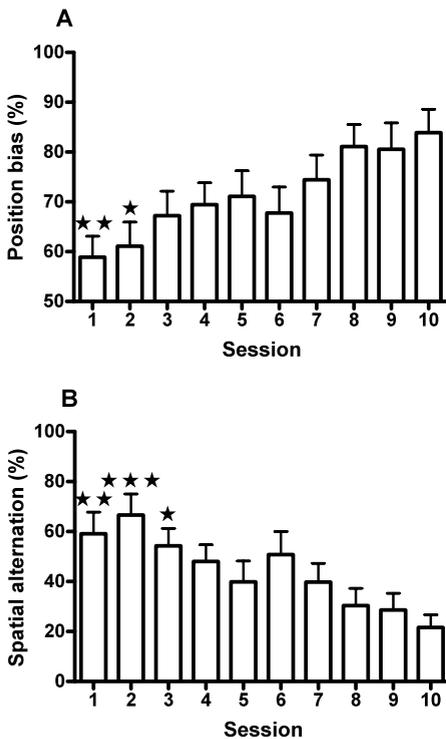


Fig. 3. The percentage position bias and percentage spatial alternation in the 10 sessions of the modified Krechevsky paradigm (n = 9). Data represent mean ± S.E.M. A. Position bias. B. Spatial alternation. ***: significantly different from session 10 ($p<.001$), **: significantly different from session 10 ($p<.01$), *: significantly different from session 10 ($p<.05$).

Forced-choice procedure

For the T-maze a significant difference in the percentage responding to – and choosing - the newly opened maze side was found between the 1-trial, the 10-trial, and the 100-trial challenge, when analysing all 10 trials of the challenges (ANOVA, $F(2,19)=6.84, p<.01$). There was a significantly reduced response to the newly opened side in the 100-trial challenge compared to the 1-trial challenge (Bonferroni's Multiple Comparison Test, $p<.05$) as well as the 10-trial challenge (Bonferroni's Multiple Comparison Test, $p<.01$) (Fig. 4). The results of the 1-trial and 10-trial challenges did not differ significantly from each other. When exclusively analysing the first five trials of the challenges no differences between the challenges were revealed by ANOVA. For the Y-maze a significant difference in the percentage responding to – and choosing - the newly opened side was found between the 1-trial, the 10-trial, and the 100-trial challenge. Differences were found when analysing all 10 trials of the challenges (ANOVA, $F(2,15)=5.69, p<.05$) as well as when analysing the first five trials of the challenges

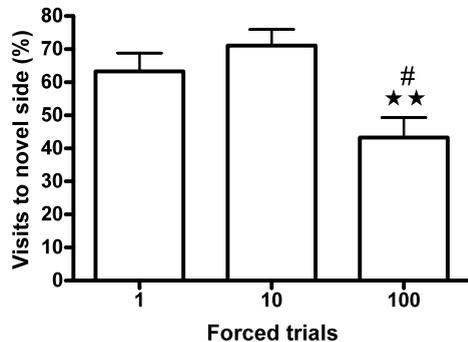


Figure 4. The percentage visits to the newly opened maze side in the forced-choice paradigm in T-maze (n = 8). Results after 1, 10 or 100 forced trials (the 1-trial, 10-trial and 100-trial challenge). Data represent mean ± S.E.M. All 10 free trials of the challenges are included. #: significantly different from the 1-trial challenge ($p<.05$). **: significantly different from the 10-trial challenge ($p<.01$).

(ANOVA, $F(2,15)=12.70$, $p<.001$). When analysing all 10 challenge trials there was a significantly reduced responding to the newly opened side in the 100-trial challenge compared to the 10-trial challenge (Bonferroni's Multiple Comparison Test, $p<.05$) (Fig. 5A). Likewise, for the first five challenge trials there was a significantly reduced responding to the newly opened side in the 100-trial challenge com-

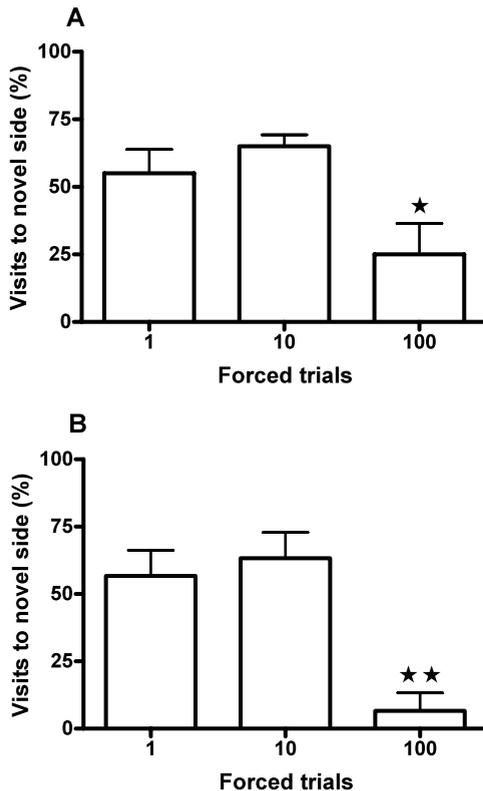


Figure 5. The percentage visits to the newly opened maze side in the forced-choice paradigm in Y-maze ($n = 6$). Results after 1, 10 or 100 forced trials (the 1-trial, 10-trial and 100-trial challenge). Data represent mean \pm S.E.M. A. All 10 free trials of the challenges are included. B. First five trials of the challenges are included. *: significantly different from the 10-trial challenge ($p<.05$). **: significantly different from the 1-trial and the 10-trial challenge ($p<.01$).

pared to the 1-trial challenge as well as compared to the 10-trial challenge (Bonferroni's Multiple Comparison Test, $p<.01$) (Fig. 5B). The results of the 1-trial and 10-trial challenges did not differ significantly from each other in any of the analyses.

Discussion

In the present modified version of Krechevsky's classic paradigm (Krechevsky, 1932), rats were allowed for a large number of trials to choose freely between the right and left arm of a T-maze. Each arm contained one of two different olfactory stimuli, and the rats were rewarded for all responses. The results obtained confirmed Krechevsky's original finding that rats do not behave randomly in the so-called "pre-learning phase", but exhibit highly structured behaviour. We found many examples of spontaneous behavioural persistence – or behavioural "strategies" – with less than 1 % probability of these occurring by chance (i.e. eight consecutive responses according to the same strategy, Fig. 1A-C)). Our hypothesis that rats would show spontaneous behavioural persistence in this paradigm was thus confirmed. The present study also demonstrated – for the first time – that rats developed spontaneous behavioural strategies using olfactory stimuli.

The behavioural pattern of a selected rat, shown in Fig. 2, closely resembles a type of behavioural pattern that Krechevsky demonstrated in rats and that he used as evidence for systematic problem-solving behaviour ("hypotheses") in rats: the rat on the first session responds randomly according to the position dimension. However, this result reflects the fact that the rat behaves 89 % in accordance with a spatial alternation pattern. After the initial spatial alternation behaviour the rat shifts to another kind of response pattern, i.e. it starts responding well over chance level to the right (sessions 2-7), followed by a sharp shift to a clear "go left" pattern on sessions 8-10.

Krechevsky originally proposed that this kind of behavioural structuring represented the testing of problem-solving "hypotheses" – or attempted solutions – by rats (Krechevsky, 1932; Tolman and Krechevsky, 1933). He believed various "hypotheses"

would be tested by the rat until the correct solution of the problem was found. Krechevsky in his paradigm – in contrast to the present version of the paradigm - rewarded rats randomly for their responses, not reinforcing any particular response pattern, and no behavioural pattern was therefore “correct”. Later it has been demonstrated, that the same kind of behavioural structuring takes place when all responses are rewarded – as in the present study - and no “problem” therefore is posed to the rats. The behavioural structuring therefore cannot reflect testing of problem-solving “hypotheses” as Krechevsky believed (*Witkin, 1942*), but is a more general spontaneous behavioural phenomenon. The results from the present study supports this interpretation as we rewarded all responses and nevertheless found systematic behaviours – or behavioural “strategies” - in the rats. Given the fact that the behavioural structuring does probably not reflect the testing of problem-solving “hypotheses” in rats, it is open to discussion if the behavioural structuring necessarily implies a cognitive interpretation, in the sense that the behaviour is a result of cognitive processes and are initiated and controlled from within the animal. The structured response sequences can probably also be explained as created by initially random choices that are repeated in sequences because they are being reinforced on a FR1 schedule.

With regard to the types of strategies developed by the rats, simple position or spatial win-stay strategies (“go right” or “go left” strategies) dominated except in the earliest testing phase (Fig. 1A-C). In early testing, spatial alternation (win-shift strategies) seemed to be predominant. The shift from spatial alternation tendencies towards position strategies was also reflected by the whole-session parameters (Fig. 3A-B). Significantly higher position bias and lower spatial alternation rates were found in the last session compared to a number of earlier sessions. For olfactory responses and olfactory alternation there was no significant difference between sessions. Since Krechevsky was only interested in analysing individual data, no direct comparisons can be made with his studies regarding

this shift in the type of strategies occurring. It is well-known from spontaneous alternation research that rats have a tendency to engage in spatial alternation during initial running in a T-maze (*Montgomery, 1952; Lalonde, 2002*). However, spontaneous alternation methods are not directly comparable to the present paradigm as spontaneous alternation is performed without the extra sensory stimuli used in the Krechevsky paradigm. Spontaneous alternation is traditionally regarded an exploratory phenomenon and is usually not considered a spontaneous strategy (*Montgomery, 1952; Lalonde, 2002*). Since all responses were rewarded with food in the present Krechevsky paradigm, the spatial alternation behaviour in this paradigm can also be characterised as win-shift behaviour. Win-shift foraging strategies are preferred by a number of species (*MacDonald, 1994*). E.g. it has been demonstrated using baited radial arm mazes that rats spontaneously use win-shift strategies in these types of mazes (*Olton & Samuelson, 1976*). Krechevsky emphasised that the position strategies developed in his experiments are not the result of simple spatial bias of the kind that can, for instance, be forced upon the animals by a less perfectly controlled situation. The results of the present experiment support this claim, as rats with high position responding would often switch the preferred side between sessions. The occurrences of repetitive position responding towards the end of the testing period must therefore be characterised as win-stay strategies rather than behaviour induced by simple spatial bias.

Olfactory stimuli were introduced in the present paradigm instead of the visual stimuli used by Krechevsky. We though it likely that the behaviour of rats would be at least as strongly influenced by olfactory stimuli as by visual stimuli, and expected that rats would develop olfactory strategies. Previously we had established by use of learned discriminations that rats could fully discriminate between the olfactory stimuli when presented in the same kind of odour bars. As can be seen in Fig. 1B, olfactory strategies did occasionally form, but less frequently than position and spatial alternation stra-

gies. Furthermore, the olfactory strategies were not as long-lasting as the spatial strategies could be. The pseudo-randomisation of the olfactory stimuli between right and left ensured that the same odour was never presented more than three times in a row to the same side of the maze. However, the olfactory stimuli could be presented in an alternating fashion between right and left for up to seven trials in a row. This opens the possibility that some of the detected olfactory strategies and olfactory alternation strategies could be secondary to rats engaging in spatial strategies (i.e. position strategies for olfactory alternation strategies and spatial alternation strategies for olfactory strategies). Certainly, there were a few examples in which rats engaged in longer-lasting spatial alternation strategies at the time olfactory strategy sequences were detected. These are marked on Fig. 1B. Furthermore, a number of short-lasting olfactory alternation sequences were found towards the end of the experiment in the middle of much longer-lasting position strategies. The Krechevsky paradigm could possibly be useful in rat models of OCD - e. g. pharmacological OCD models (*Korff & Harvey, 2006*) - as the paradigm models the natural balance between spontaneous behavioural persistence and shifting.

In the forced-choice paradigm we intended to create a response habit in rats in a T/Y-maze by blocking one maze arm and letting the animals run down the other arm for 100 trials. Subsequently, both arms were opened for 10 trials and it was noted which arm the rats would select when allowed to choose freely. After 100 forced trials of running to the same side of the maze we did see a significant tendency of rats to keep choosing that side, compared to when only 1 or 10 forced trials had been given (Fig. 4-5). This result was achieved for the T- as well as Y-maze. We thus confirmed our hypothesis saying that the habits could be created in rats by the procedure.

In several of the earlier experiments addressing the characteristics of habits, the main subject has been overtraining transfer effects such as the controversial overtraining reversal effect (*Sutherland and Mackintosh, 1971; Mackintosh, 1974*). The overtraining

literature has documented many effects of overtraining, some facilitating and some inhibiting on later response shifting. Even though the present experiment also deals with the tendency to shift response after different training periods, the results obtained with the overtraining experiments cannot be said to be directly comparable. The animals in the overtraining paradigms, in contrast to the rats of the present paradigm, learned a response by asymmetric reinforcement and avoidance responses were therefore established to competing responses. This is not the case in the present forced-choice paradigm.

Theoretically the learning of a response is believed to have two stages, an initial "action" stage and a later "habit" stage (*Dickinson, 1985*), or in the terminology of Norman & Shallice (*1986*), an initial stage of "controlled actions" followed by a stage of "automatic actions". In the initial "action" stage, according to Dickinson (*1985*), the action is flexible and goal directed, i.e. controlled by cognitive knowledge about its relation to the goal. Norman & Shallice stress that only during initial learning, does the performing of the response require attentional resources from a cognitive "supervisory attentional system". In the later stage the response is believed to develop into a more inflexible habit (*Dickinson, 1985*) or automatic schema (*Norman & Shallice, 1986*). In that stage the response is automatically triggered by stimuli without cognitive or attentional control (*Norman & Shallice, 1986*) and furthermore is independent of the value of the goal (*Dickinson, 1985*).

In the present study the response during 100 forced trials became somewhat automatic and inflexible as rats after that amount of training acquired a reduced tendency to switch side in the free-choice challenge. However, the response did become far from fully automatic. All rats except one visited the newly opened arm at least once during the 10 free trials of the 100-trial challenge. In the Y-maze the tendency of rats to repeat the highly rehearsed response was especially pronounced during the first five trials of the 100-trial challenge, while it was distributed over all 10 challenge trials in the T-maze. For the T-maze

no significant difference between challenges was revealed when analysing only the first five challenge trials. It is not surprising that differences between mazes can be found. The ease in which habits are disturbed by competing exploration tendencies, for instance, is probably different for different mazes. The results of a recent study indicate that more than 200 forced-choice trials are necessary to create a truly automatic habit (Moustgaard & Hau, 2008). However, it may also be the case that habits created by forced-choice procedures are in general easily disrupted by exploration tendencies. The statistical analysis did not reveal any habit formation after 10 forced trials; instead a non-significant increase in visits to the newly opened side was found, compared to the situation after only one forced trial.

The Krechevsky paradigm as well as the forced-choice paradigm could be useful for studying the neural substrate of spontaneous behavioural persistence and habit formation, as well as the effect of neuroactive drugs on these functions. The Krechevsky paradigm models the natural balance between spontaneous strategy formation and shifting. One can imagine that this balance could be disturbed by neuroactive drugs or brain lesions. The forced-choice paradigm is an alternative to asymmetric reinforcement training methods for modelling habit formation. Both of the presented paradigms are potentially useful for modelling aspects of pathological behavioural persistence as for instance seen in human OCD.

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