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Research report

Relationship of delay aversion and response inhibition to extinction learning, aggression, and sexual behaviour

Filip Van den Bergh [a,b,*], Marjolein Spronk [a], Leila Ferreira [a], Emilie Bloemarts [a], Lucianne Groenink [a,b], Berend Olivier [a,b,c,d], Ronald Oosting [a,b]

[a] *Section Psychopharmacology and Utrecht Institute for Pharmaceutical Sciences (UIPS), Department of Pharmaceutical Sciences, Faculty of Science, Utrecht University. Sorbonnelaan 16, 3584CA Utrecht, The Netherlands*
[b] *Rudolf Magnus Institute of Neuroscience, Department of Psychiatry, University Medical Center Utrecht, The Netherlands*
[c] *Department of Psychiatry, Yale University School of Medicine, New Haven, CT, USA*
[d] *PsychoGenics Inc., 765 Old Saw Mill River Road, Tarrytown, NY 10591, USA*

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Abstract

Impulsivity is an important symptom of many psychiatric disorders, and can be divided into two subtypes: response inhibition deficits and delay aversion. In the present study, we investigated the relationship between delay aversion and response inhibition, both to each other and to locomotion, extinction of conditioned responses, sexual behaviour, and aggressive behaviour. To that end, we quantified the behaviour of 24 rats in several tests. To measure response inhibition, rats were trained in a stop-signal task. In this operant task, rats were rewarded food if they inhibited execution of a response after presentation of an audible stop-signal. Delay aversion was measured in an operant task in which rats made a choice between a small, immediately available reward and a large reward available after a delay. The results showed that delay aversion and response inhibition were independent. Responses during extinction and various measures of aggressive behaviour were positively correlated to delay aversion. The speed of go-trials in the stop-task was correlated to non-aggressive behaviour. We conclude that the role of response inhibition in various behaviours is small, but delay aversion in particular contributes to several other behaviours, such as aggressive behaviour and extinction.

Keywords: Stop-signal task; Delayed reward task; Extinction test; Impulsivity

1. Introduction

Some situations call for rapid responding based on little information, and people and animals are well equipped for such situations. However, if this rapid responding is applied to situations where forethought is required, behaviour may become impulsive and may seriously hamper everyday life [1]. Recent research suggests that at least two different processes may lead to impulsive behaviour [2]. Delay aversion is the first process leading to impulsivity. Impulsive individuals perceive delays as especially aversive, and therefore make decisions resulting in immediate gratification, or, if delays are unavoidable, avert attention from the long-term goal to decrease the subjective delay [3–6]. Intolerance to delayed rewards may be the result of alterations in the frontostriatal reward networks, including the nucleus accumbens core [7,8]. In the second theory, impulsivity is the result of a failure to inhibit ongoing or planned responses [9]. This process is often described as a competition between hypothetical go- and stop-signals in which the winning signal determines whether or not a response is made [the horse-race model: 10]. Frontal and medial striatal areas are implicated in inhibiting prepotent responses [8,11,12].

The two impulsivity subtypes are core symptoms of many psychiatric disorders. In preschool children suffering from attention-deficit hyperactivity disorder (ADHD), delay aversion is especially prominent, occurring alone in 27% of the children, and in 29% together with a response inhibition deficit [13,14]. Further, heroin and cocaine abusers display delay aversion [15,16], and a similar delay aversion is seen in smokers [17,18] and alcoholics [19]. Delay aversion is not just associ-

* Corresponding author at: Section Psychopharmacology and Utrecht Institute for Pharmaceutical Sciences (UIPS), Department of Pharmaceutical Sciences, Faculty of Science, Utrecht University. Sorbonnelaan 16, 3584CA Utrecht, The Netherlands. Tel.: +31 30 253 1599; fax: +31 30 253 7387.
E-mail address: f.s.vandenbergh@gmail.com (F. Van den Bergh).

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ated with addiction to drugs, as it predicts pathological gambling severity as well [20,21], suggesting that it is not the drugs causing changes in delay tolerance, but rather the trait causing susceptibility to addiction. Furthermore, a recent study showed that delay aversion predicts the acquisition of cocaine self-administration in rats [22]. A shared underlying core deficit may also explain the high incidence of comorbid ADHD and substance-abuse disorders [23,24]. An association has also been found between delay aversion and classroom observations of aggressive behaviour [4]. However, the association between delay aversion and aggression has not yet been extensively studied.

Response inhibition also plays a central role in ADHD, occurring alone in 15% of preschool patients and together with delay aversion in another 29% [13,14]. The response inhibition deficit in ADHD patients is well studied across all ages, including adults [25–27]. Other disorders in which response inhibition plays an important role are oppositional defiant disorder (ODD) and conduct disorder (CD) [28,29]. Descriptions of impulsive aggression (such as 'hair-trigger' [30]) suggest an inability to inhibit aggressive urges and thus a potential involvement of response inhibition.

Clearly, both delay aversion and response inhibition are central traits important to many behaviours, both normal and pathological. Before the two impulsivity subtypes were recognized as complementary, many studies were aimed at reinforcing one theory as the main or core symptom of a disorder [3,9]. Now that delay aversion and response inhibition are perceived as independent contributors to impulsivity, studies have focused on finding differences and similarities between the two subtypes [2,5,13], and determination of the relative contributions of both impulsivity subtypes to pathological behaviour [4]. A disadvantage of the groups used in those studies is their heterogeneity. The variability within children diagnosed with ADHD can be very large, in part because both impulsivity subtypes can lead to ADHD symptoms [31].

The aim of the present study is to determine the relationship between delay aversion and response inhibition and their involvement in various other basal behaviours. To that end, we quantified the behaviours of 24 untreated rats in a number of different tests. This approach can uniquely be used to determine the overlap between the two impulsivity subtypes because the experimental group is very homogeneous compared to human samples. Further, near-absolute control can be executed over the environment of the animals. Therefore, any associations are likely to be the result of actual overlap between the two impulsivity constructs. Finally, the influence of the two impulsivity subtypes on a number of other basal behaviours important for animal survival can reliably be measured.

2. Methods

2.1. Animals and housing

Twenty-four male Wistar rats (HsdCpb:WU) obtained from Harlan (The Netherlands) weighing 125 g on arrival, were housed in a light (lights on from 7:00 to 19:00), temperature ($21 \pm 2\,^{\circ}C$), and humidity ($50 \pm 10\%$) controlled animal facility. At the start of the study, they were housed in groups of four male rats. At this stage, animals received 15 g/day/rat of standard laboratory chow and free water. This food restriction served as an incentive for responding in the operant tasks (the stop-signal task, the delayed reward task and the extinction test). After approximately 8 months, the groups of four male rats were split and each rat was housed in a cage together with a female companion. At this point, animals received free food and water. One animal died of an unknown cause during the stop-signal task procedure (within 1 month after arrival). The ethical committee on animal experiments of the Faculties of Pharmaceutical Sciences, Chemistry and Biology of Utrecht University approved the experiments.

2.2. Apparatus

The stop-signal task and the extinction test were conducted in a set of eight Med Associates operant chambers controlled by MED-PC IV software (MED Associates, Vermont, USA). Food rewards delivered in the operant chambers were 45 mg Research Diets (USA) NOYES precision pellets (PJPPP-0045) obtained from Sandown Chemical Limited (England). The operant chambers were equipped with a lever and a signal lamp on each side of the food magazine. An additional signal lamp was mounted above the food magazine. Tones were presented using a speaker mounted near the ceiling of the box. The delayed reward procedure was conducted in a different set of eight Med Associates chambers equipped with a curved five-hole nosepoke wall, but lacking levers. The open field consisted of a gray PVC box ($l \times w \times h$: 75 cm × 75 cm × 40 cm) with a camera mounted in the ceiling of the test room. Up to four rats could be tested at the same time. The observation boxes used in the sexual and aggressive behaviour tests were rectangular, grey PVC boxes with one transparent side ($l \times w \times h$: 60 cm × 30 cm × 40 cm) and sawdust bedding on the floor. For the aggressive behaviour tests, a transparent, perforated division was used to divide the box in two compartments, the largest consisting of approximately three-quarters of the box.

2.3. Experimental design

The group of 24 rats was followed over a year and tested in many different tests for impulsivity and other possibly related constructs. The order of the different tests was the same for all animals and is described below. The order in which animals were tested on a day was varied for each test to avoid effects of time-of-day. Measurements used for this study were always at least 1 week apart. All operant procedures are available for download at the Medstate Notation Repository (http://www.mednr.com).

The order of tests and the time animals required to complete the training and tests: stop-signal task (4 months); delayed reward task (2 months); open field test (1 week); extinction (2 weeks); sexual behaviour (1 month); aggressive behaviour (1 month); testosterone collection (terminal experiment).

2.3.1. Stop-signal task

The stop-signal task was adapted from Eagle and Robbins [32]. Animals were placed in the operant chambers for 60 min or until they had completed 200 trials. Sessions were divided into blocks, which consisted of several successful go-trials (1–3, determined randomly), and a concluding stop-trial. Lever extensions and food rewards were signalled by the illumination of a light above the lever or feeder tray. At the start of a go-trial, the left lever was extended for a maximum of 60 s. A response on the left lever resulted in the retraction of that lever and extension of the right lever for a limited amount of time (the limited hold period), during which the animal had to make a response to receive a food reward. If the animal failed to respond within the limited hold period, an omission was scored, and the animal received a timeout. Stop-trials were similar to go-trials, except for a 400 ms tone that was presented immediately, or 800, 700, 600, or 500 ms before the expected response on the second lever (based on previous sessions for each animal individually, as described below). On stop-trials, animals had to inhibit their response on the second lever for the entire limited hold period to receive a food reward. Failure to do so resulted in a timeout. During timeouts, the houselight was extinguished for 5 s. After the timeout period, the inter-trial interval commenced automatically. The duration of the limited hold period was determined for rats individually, and was based on their previous performance. The limited hold period was defined as the maximum mean time between pressing the left lever and the right lever

plus 150–300 ms, and ranged between 850 and 1500 ms. Three measures were derived from the stop-signal task. First is the mean go response time (mRT). Second is the stop-signal response time (SSRT), calculated according to Logan [10]. The SSRT was defined as the mean of the individual SSRTs calculated for each stop-signal interval. The final measure is the corrected inhibition ratio as described in Tannock et al. [33]. The corrected inhibition ratio is a measure for the success of response inhibition that takes into account that in a number of trials (proportional to the number of omissions during go-trials) animals would not attempt a response. Training for the stop-signal task took approximately 4 months.

2.3.2. Delayed reward task

The delayed reward task was adapted from Cardinal et al. [34]. In a session consisting of six blocks of eight trials, rats had a choice between a nosepoke hole that, if the rat poked in the hole using its nose, delivered a single food reward instantaneously, and a second nosepoke hole that delivered four food rewards, but after a delay. In the first block, this delay was 0 s, but in each successive block the delay was increased until it was 60 s in the final block (0, 5, 10, 20, 30 and 60 s). To make sure that the rats had actually sampled both options, the first two trials of each block were forced trials in which only one of the holes was illuminated. Both options were presented once in the forced trials, and the order of presentation was determined randomly. The remaining six choice trials were used to calculate a preference ratio for each delay. At the end of the training period, performance had stabilized (number of responses/percentage choice for the large reward per block: 0 s, 6/74%; 5 s, 6/63%; 10 s, 6/45%; 20 s, 6/42%; 30 s, 6/28%; 60 s, 6/21%) From these six ratios, the preference curve was drawn, and the area under the preference curve (AUPC, which varies from 0 to 60) was calculated. The AUPC is a theory-neutral measure for inhibition in the delayed reward task [35]. Training for the delayed reward task took approximately 2 months.

2.3.3. Open field test

Animals were placed in the open field for 15 min. Noldus Ethovision [36] was used to track the animals and calculate the distance moved. The open field was repeated twice and the average was taken as an index of locomotion.

2.3.4. Extinction

After the open field test, animals were trained on a continuous reinforcement schedule for two days, which all animals learned readily. On day 3, none of the levers resulted in the delivery of food rewards, and the number of responses made in a 30 min session was registered.

2.3.5. Sexual behaviour

The sexual behaviour procedure was adapted from Pattij et al. [37]. After the extinction test, the male animals were housed apart from each other and a companion female was introduced (see Section 2.1). Twice a week for 2 weeks, the male rats were put in an observation cage for 1 h. In the second half of that hour, a naive female rat was introduced. To induce receptivity, the females were pre-treated with 50 μg estradiol 36 h in advance. Mounts, intromissions and ejaculations of the male rat were observed using Noldus Observer [38]. The first three sessions were considered training sessions, and only the data of the fourth test were used for this study.

2.3.6. Aggressive behaviour

Animals were tested for aggression twice a week for 2 weeks. Male rats together with their female companions were put in an observation cage 24 h before testing. At the start of the test, the female was removed from the observation cage, and an intruder rat (weighing ∼100 g less than the resident) was placed inside a shielded compartment in the observation box (see Section 2.2). Each intruder was used only once. After 10 min, the division was removed, and all behaviour was scored manually using Noldus Observer [38]. The following behaviours were scored from the perspective of the resident: bites, fight sequences, ano-genital sniffs, grooming by the resident of the intruder, and mounts. The last three behaviours were considered non-aggressive. Afterwards, intruders were sacrificed, shaved, and the total length of all wounds added was measured using a marking gauge (expressed in mm). Again, only the data of the fourth test were used.

2.3.7. Testosterone

Blood was collected following decapitation between 10 and 12 a.m. Blood plasma testosterone was determined using an MP Biomedicals Inc. (Orangeburg, NY, USA) ImmuChem^{TM} Double Antibody ^{125}I RIA kit. Measurements were the average of three assays determined using an optimal standard curve.

2.4. Statistics

All variables were inspected for normality and then correlated to measures of inhibitory control and delay valuation using Pearson' product moment correlation coefficient. While normality can be tested using the Kolmogorov–Smirnov test, this test assumes normality unless this hypothesis is rejected. As such, many different factors may contribute to not finding such an effect (for example, a small sample), and as a result the test is not as exact as it appears. To resolve this problem, we combined visual inspection with the Kolmogorov–Smirnov test. For correlations to be considered, they had to be significant (with the level of significance set at 5%, one-tailed) as well as larger than 0.45, resulting in an explained variance (r^2) of at least 20%.

3. Results

As is clear from Fig. 1 neither the speed of the stop-process nor the speed of the go-process is related to delay aversion. Neither the SSRT nor the mRT were correlated with the AUPC ($r = 0.06$, NS and $r = 0.08$, NS, respectively). Similar findings are reported in humans [13,14], although in some reports go response time is mildly correlated to inhibition in a delayed reward task [4].

The correlations between the measures of impulsivity and the remaining measures are listed in Table 1. The speeds of the go- and the stop-processes are correlated ($r = 0.44$, $p = 0.019$). Although this correlation did not reach our criterion ($r \geq 0.45$), it may indicate that both processes are affected by a third, underlying factor. Like the stop-signal task in human subjects, the SSRT is related to the corrected inhibition rate ($r = -0.64$, $p = 0.001$), with slower inhibition response times resulting in lower inhibition success [4].

The distance moved in the open field test was not associated with any of the measures in the stop-signal task, but was mildly correlated to the behaviour in the delay aversion task ($r = -0.37$, $p = 0.05$). Although significant, we think this effect is too small to be of importance. The number of lever presses during the extinction session was also not correlated to any of the stop-

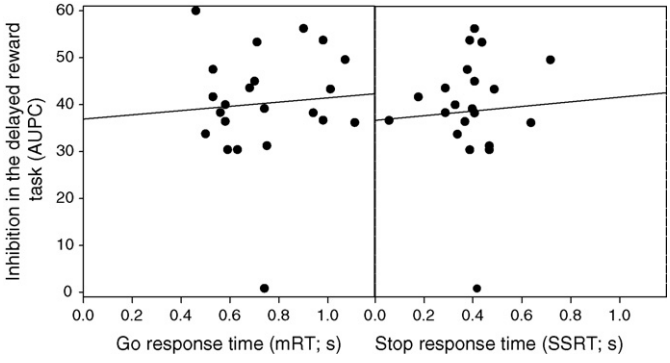

Fig. 1. Correlations between two measures of impulsivity. Used measures were the stop-signal task (the go response time mRT and the stop response time SSRT) and the delayed reward task (the area under the preference curve AUPC). The correlations were not significant (left, $r = 0.08$; right, $r = 0.06$).

Table 1
Correlations between measures of impulsivity and other relevant measures

Measure	Mean ± S.E.M.	Go response time	Impulsivity in stop-task (SSRT)	Impulsivity in delayed reward task (1-AUPC)
Stop-signal task				
Go response time (mRT; s)	0.74 ± 0.04	–	0.44#	−0.08
Stop response time (SSRT; s)	0.38 ± 0.03	0.44#	–	−0.06
Corrected inhibition rate (%)	63 ± 5	−0.23	−0.64*	−0.15
Delayed reward task				
Inhibition (AUPC)	40.3 ± 2.6	0.08	0.06	–
Miscellaneous behaviours				
Distance moved (m)	48.1 ± 1.8	−0.30	0.00	0.21
Extinction (responses)	92.4 ± 8.6	−0.12	−0.01	0.63*
Sexual behaviour				
Number of mounts	23.0 ± 4.9	−0.22	0.11	−0.38#
Number of intromissions	14.5 ± 1.3	0.32	0.02	0.02
Number of ejaculations	2.9 ± 1.4	0.31	−0.02	−0.09
Aggressive behaviour				
Number of bites	6.4 ± 1.4	0.05	0.04	0.60*
Number of fights	4.2 ± 0.8	0.02	−0.15	0.52*
Total wounds (mm)	22.2 ± 4.6	−0.09	0.04	0.50*
Non-aggressive behaviours	20.0 ± 2.2	0.55*	0.07	0.03
Testosterone				
Plasma	1.13 ± 0.12	−0.16	−0.30	0.07

All measures were correlated with two measures of the stop-signal task (the go response time mRT and the stop response time SSRT) and the delayed reward task (the area under the preference curve AUPC). * indicates a significant correlation, # indicates a correlation that reached statistical significance but did not meet the absolute criterion ($r > 0.45$, resulting in an explained variance >20%; see Section 2.4).

signal task measures, but the correlation with delayed reward task performance was quite strong ($r = -0.63$, $p = 0.001$).

None of the three sexual behaviour parameters (mounts, intromissions and ejaculations) were related to any of the impulsivity measures. While a small correlation exists between the latency to the first mount and the AUPC ($r = -0.38$, $p = 0.05$), this effect did not meet our criterion and is thus regarded as behaviourally not relevant or even spurious. Further exploring the relationship between sexual behaviour and impulsivity did not yield any effects (latency to the first occurrence of each of the three sexual behaviours and the number of intromissions per ejaculation). Although the correlations between delay aversion and both sexual behaviour and locomotion did not reach criterion, it did raise the question whether sexual behaviour and locomotor activity are correlated. Our results show that the number of mounts was not correlated to the distance moved in the open field ($r = 0.16$, NS), however, the number of ejaculations was ($r = -0.46$, $p = 0.01$). In other words, hyperactive animals have fewer ejaculations in a 30 min sexual behaviour test.

A relationship between impulsivity and aggression was apparent in many of the different indexes for aggression. All non-aggressive social behaviour in the test for aggressive behaviour correlated with the go response time (mRT) of the stop-signal task (sum: $r = 0.55$, $p = 0.004$; ano-genital sniffs: $r = 0.58$, $p = 0.002$; grooming: $r = -0.43$, $p = 0.02$; mounts: $r = 0.48$, $p = 0.01$). Thus, animals that made slower go-responses in the stop-signal task display more ano-genital sniffs and mounts, but less grooming behaviour towards the other male in the test for aggressive behaviour. In contrast, all aggressive behaviours in this test correlated negatively with the AUPC (bites: $r = -0.60$, $p = 0.002$; fights: $r = -0.52$, $p = 0.006$; wounds: $r = -0.50$, $p = 0.009$). This means that animals that display delay aversion are also aggressive in the resident–intruder test. The number of non-aggressive behaviours was not related to the number of aggressive acts.

Testosterone levels in the blood were not associated to both impulsivity subtypes. In addition, basal plasma testosterone was not associated with sexual performance or basal aggression [see also 39].

4. Discussion

The present article shows that response inhibition is unrelated to delay aversion in a homogeneous group of rats. In children, a similar lack of association has been reported in several studies. Dalen et al. [13] found a lack of association in 3-year-old children tested on a delay aversion task (in which subjects could choose between one sweet delivered after 1 s or two sweets delivered after 17 s) and a go–no go inhibition task. Sonuga-Barke et al. [14] have shown that response inhibition deficits are unrelated to delay aversion in 3–5.5-year-old children. Solanto et al. [4] obtained similar results using the delayed reward task and the stop-signal task in 7–9.9-year-old children. The present study, using correlational research in animals also supports the conclusion that impulsivity is not a unitary construct. One of the added values of the present study lies in the homogeneity of the experimental group. All rats were members of the same outbred strain, and had received similar treatment throughout their life.

As a result, the correlations in the present study are less disturbed by unknown factors, allowing for a more accurate estimation of the overlap of the separate impulsivity constructs. Winstanley et al. [40] reported that delay aversion is uncorrelated to premature responding in the five-choice serial reaction time task, an animal analogue to the continuous performance task in humans [41]. The exact type of impulsivity measured in the five-choice serial reaction time task is still under scrutiny, however, and the measure is often referred to as "aspects of response inhibitory control" [42].

In human life, impulsivity may play a detrimental role. We investigated the correlation of the two impulsivity types to several behaviours important to everyday life (of a rat), such as locomotion, learning, aggression, and sexual behaviour. The advantage of the present design is that by measuring within the same animals and calculating correlations, we quantified the magnitude of the relationship between delay aversion and aggression.

Spontaneous locomotor activity was not associated with either of the impulsivity subtypes. In children with ADHD, however, Sagvolden et al. [3] found that hyperactivity may be the result of delay aversion. Children with ADHD developed hyperactivity in situations where the reward was delayed or not delivered at all (such as under extinction). Because no rewards are withheld and no such pressure is present in the open field, we showed that general locomotor hyperactivity is not related to delay aversion, although specific situations such as that described above may still induce hyperactivity. This is further illustrated by the extinction sessions of the present experiment. During extinction training a reward was withheld, and an association was found in the current dataset between extinction responding and tolerance to delayed rewards. Animals that displayed a preference for immediate gratification in the delayed reward task also displayed persistent lever-pressing during the extinction session. Persistence during extinction is also one of the clearest defects in the SHR strain [43–45], a strain often used as a model for ADHD [46,47]. Previous research in our lab has shown that extinction is also highly (up to 0.80) correlated to burst responses in the differential reinforcement of low rate responding (DRL)-72 s task [45]. Because no direct comparisons between the DRL and the delayed reward task exist, any association is speculative. However, in addition to their persistence during extinction, SHR also show an increased number of burst responses in the DRL [45].

In spite of the importance of dopamine and the reward circuitry in the motivational aspects of sexual behaviour [48–50] and the involvement of dopamine and those same brain areas in delay aversion [7,34,51], sexual dysfunctions such as premature ejaculation, low sex drive, or hypersexual activity are not reported to be related to ADHD or other impulsivity disorders. This independence is also reflected in the current data, as none of the correlations between impulsivity measures and parameters of the sexual behaviour test reached our criterion. Some reports do exist that ADHD patients have more sexual impulsive disorders, including paraphilias [52], but such disorders are not reflected in the used animal models.

In the aggressive behaviour test, a male was introduced into the territory of the resident. Animals that responded slowly in go-trials of the stop-signal task displayed more ano-genital sniffs and mounts, but less grooming behaviour directed at the intruder than faster animals do. Why the direction of the correlation between go-trial speed and grooming behaviour is opposite to the direction of the correlation found between the other two non-aggressive behaviours is unclear. This difference may be the result of different styles of social behaviour found in fast versus slow responding animals. While the non-aggressive behaviours were correlated to the go-trial speed, the three measures of aggression correlated to tolerance to delayed rewards. Animals that chose immediate gratification were more aggressive and injure their opponents more than other animals. A similar but more modest association between delay aversion and aggressive behaviour was also found in children [4]. The association between delay aversion and aggressive acts in rats and children provide insight into the type of impulsivity involved in aggression. A universally accepted classification of aggression in humans does not exist, but impulsive aggression is usually listed as a factor [30,53,54]. It is often assumed that this type of aggression is related to an inability to inhibit aggressive urges [sometimes called "hair-trigger" responses: 30]. The association between aggression and delay aversion (and the lack of an association with stop-signal task performance) suggests that aggressive behaviour may be the result of an inability to foresee the consequences rather than a ballistic process unchecked by inhibitory control.

The correlation study described above provides further evidence for the independence of response inhibition and delay aversion. In addition, it provides evidence that both subtypes independently contribute to other behaviour. The final line of reasoning for the independence of these impulsivity subtypes comes from their pharmacological differentiation. Psychostimulants have been shown to have anti-impulsive effects in healthy animals in the delayed reward task [34,51], while impulsivity in the stop-signal task is unaffected [11] or elevated (Van den Bergh et al., submitted for publication). Most psychostimulants are dopamine reuptake inhibitors and releasers, but also inhibit the noradrenalin and the serotonin transporter [55]. Dopamine reuptake inhibition may decrease delay aversion [34], while noradrenalin reuptake inhibition may be the active component for the positive effects of psychostimulants in the stop-signal task [56]. Research should therefore focus on specific pharmacological treatments for the subtype of impulsivity a patient displays.

The pharmacological dissociation between delay aversion and response inhibition deficits is not always clear-cut. While response inhibition in animals is generally disrupted after psychostimulant administration (see above), psychostimulants have been shown to decrease response inhibition deficits in humans [27]. Several causes may underlie this discrepancy. First, we compare healthy rats to human patients. Both the species and the presence of a disorder may result in different effects of D-amphetamine. The second reason for the opposite effect of D-amphetamine in humans and rats is the amount of training necessary before a measurement can be made. Human measurements are made after only several practice trials, and execution

of the stop-task is likely a controlled process. Rats often train for several months, leading to an automation of task execution. Automated behaviour is more resilient to outside interference [57,58], and D-amphetamine will therefore have no beneficial effects until the dose is so high performance collapses due to non-specific motor effects. Thus, performance-enhancing effects of D-amphetamine may be difficult to find in highly trained behaviour.

From the current study, a pattern emerges in which both delay aversion and response inhibition play important but independent roles in many different types of behaviour. The results indicate that especially delay aversion is an important construct underlying many other types of behaviour, including extinction and aggression, and is possibly more central to many behaviours than response inhibition. Rubia [59] argues that the delayed reward test is such a prominent feature of animal-inspired theories of impulsivity and ADHD because this test is the only available test in rats. This report and others however, show that many more tests for impulsivity exist in rats, some of them very similar to tests used in humans [11,32,60]. The delayed reward construct, however, is so prominent, because it is so valuable. Predictive validity of the delayed reward test is high, and the test correlates very well to other measures of impulsivity. This is true not only in animals (as shown in the present study), but also in human subjects [4,5]. A study of 51 hyperactive children and 119 controls found that hyperactivity was associated with delay aversion, while inhibition was not altered [5]. Finally, Solanto et al. [4] conclude that "delay aversion is associated with a broad range of AD/HD characteristics whereas inhibitory failure seems to tap a more discrete dimension of executive control."

The present data strongly suggest a relationship between aggressive behaviour, extinction and delay aversion, a specific type of impulsive behaviour. These findings allow us to re-think the importance of delay aversion impulsivity.

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