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Rats and Humans Paying Attention:

Cross-Species Task Development or Translational Research

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Abstract

Substantial gains have been made on the neurobiology of attention from systems neuroscience work in animal models and human cognitive neuroscience. However, the integration of rodent-based research on the specific neurotransmitter systems that subservise attention with the results from human behavioral and neuroimaging studies has been hampered by the lack of tasks that validly assess attention in both species. To address this issue, an operant sustained attention task that has been extensively used in research on the neurobiology of attention in rats was re-designed and validated for use in humans. Although humans showed better performance overall, the two species showed similar effects of several attention-related variables, including the introduction of distractor-related challenge. This task provides a useful tool for integrative, cross-species research, and may help to determine how specific neurotransmitter systems contribute to the hemodynamic changes observed in human functional neuroimaging experiments.

Keywords

sustained attention; rat; human; distraction; cross-species

Animal models play a critical role in research designed to determine the neuronal bases of cognition and behavior. In particular, animal research provides a degree of experimental control and precision not usually feasible in studies using human subjects, as well as avenues for manipulating and monitoring specific neurotransmitter and receptor systems. Attempts to use evidence from animal-based research to inform the design and interpretation of human studies inherently assume that different species draw on similar cognitive processes to perform tasks that are similar in terms of face validity. However, this assumption has been rarely tested, limiting the potential benefits of direct cross-utilization of evidence. Perhaps as a result, treatment approaches for cognitive disorders that are based on animal research frequently fail to translate into clinical efficacy (e.g., Sarter, 2004,2006).

This paper describes a set of studies designed to address this issue by characterizing human performance in a task (McGaughy & Sarter, 1995) that has been extensively used in rat research to determine the role of the cholinergic system in sustained attention and in responding to challenging situations that require the intentional, top-down control of attention (for review see Sarter, Hasselmo, Bruno, & Givens, 2005). Here, we compare rat and human performance patterns on the sustained attention task (SAT) under standard conditions and under distraction

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(dSAT). Our main focus is on the distraction condition, which in rats has been biologically linked to increased acetylcholine efflux and theoretically linked to an increased demand for the top-down control of attention (Sarter, Gehring, & Kozak, 2006). Our central question was whether the distraction manipulation leads to qualitatively similar performance changes across the two species, a finding which would support the idea that it taxed similar cognitive processes.

The basic rat paradigm is a signal-detection paradigm, which in most studies uses a short, centrally-presented visual signal. Signal and non-signal events are presented in a randomized order and with equal probability. The subject's task on each trial is to indicate whether or not a signal appeared by pressing the correct lever (one for hits, another for correct rejections) during the response period, which is indicated by a separate event (extension of the lever for rat studies; a distinct auditory tone for the human experiments reported here). The task includes several features (competing response rules, variable signal duration, and variable intertrial interval (ITI)) that impose a cognitive load, ensuring that even the basic version of the task cannot be successfully completed on the basis of side biases or simple response timing and instead requires directed attention to the presence or absence of the stimulus on each trial (c.f., Parasuraman and Davies, 1977; Parasuraman, Warm, & Dember 1978; Parasuraman & Mouloua, 1987). Distraction (in the form of a flashing houselight) can be introduced to challenge performance and increase the demands for top-down control (Gill, Sarter & Givens, 2000; Himmelheber, Sarter, & Bruno, 2000; Sarter et al., 2006).

The initial studies using this task in animals (Bushnell, 1999; McGaughy & Sarter, 1995; see Mohler, Meck, & Williams, 2001, for a mouse version) characterized the effects of variables that form the basis of Parasuraman's taxonomy of attention (Parasuraman & Davies, 1977; Parasuraman & Mouloua, 1987). These included the effects of signal intensity, signal duration, event rate, and distractors (see also Bushnell, 1999; Echevarria, Brewer, Burk, Brown, Manuzon, & Robinson, 2005; Newman & McGaughy, 2008). In the subsequent decade, neurobiological research using this task with rats has played an important part in establishing the role that cholinergic inputs to prefrontal regions play in signal detection and attentional shifts, particularly under challenging conditions (for review see Sarter et al., 2005; Sarter et al., 2006). For example, it has recently been shown that transient increases in cholinergic activity in the prefrontal cortex mediate the shift from internally-directed processing modes to input processing and signal detection (Howe, Parikh, Martinez, & Sarter, 2007).

Lesion and neuroimaging research with human and non-human primates generally concurs with rodent-based research in the view that fronto-parietal networks mediate elementary aspects of attention (e.g., Braver, Reynolds, & Donaldson, 2003; Hopfinger, Buonocore, & Mangun, 2000; Pessoa, Kastner, & Ungerleider, 2003; Sylvester, Wager, Lacey, Hernandez, Nichols, Smith, & Jonides, 2003). However, these studies lack the precise information that can be provided by rodent-based studies about the specific role of the cholinergic system (or other neurotransmitter systems) in that network. Recent studies that combine pharmacologic manipulations with functional neuroimaging approaches are an important step towards understanding this role (e.g., Bentley, Husain, & Dolan, 2004; Thiel, Friston, & Dolan, 2002). Even in these pharmacologic-fMRI studies, the drug manipulations affect neurotransmitter function at a very gross level both temporally and anatomically when compared to the usually more event- and region-specific action observed using contemporary electrochemical recording techniques in animals (Parikh, Kozak, Martinez, & Sarter, 2007). Further, most lesion- and neuroimaging-based attempts to understand the organization of attention and other cognitive functions focus on the *where* issues of what brain regions are involved, with limited consideration of the *how* issues related to transmitter function (e.g., Wager, Jonides, & Reading, 2004). A better integration of information across species (rodent, nonhuman primate, human) and levels of analysis (molecular, systems) would improve hypothesis generation, theory development, and practical application.

Although examples of such integration are rare, there is some precedent for this type of approach. In particular, the CANTAB (Cambridge Neuropsychological Test Automated Battery, Morris, Evenden, Sahakian, & Robbins, 1987) is used to assess a range of cognitive functions in humans and nonhuman primates. It has been very effective in establishing the role of specific transmitter and receptor systems in normal function and in diseases such as Alzheimer's, schizophrenia, and Parkinson's disease (see reviews by Fray & Robbins, 1996; Levaux, Potvin, Sepehry, Sablier, Mendrek, & Stip, 2007). Bushnell and colleagues (Bushnell, Benigus, & Case, 2003) examined rat and human performance in a simple sustained attention task similar to the task used here. They found similar performance across the two species, although there was some suggestion that human males were differently affected by trial rate (intertrial interval length) than were the other groups.

The present experiments examine rat and human performance in the McGaughy and Sarter (1995) sustained attention task under standard and distracting conditions. For each trial, the participants' task was to detect the presence or absence of a brief, sudden-onset visual signal (rather than the change in luminance to a constant signal used by Bushnell et al., 2003; c.f., Parasuraman & Davies, 1977; Theeuwes, 1991). Changes in stimulus duration were used to manipulate stimulus strength.

As described previously, we were especially interested in the effects of the distractor manipulation, which in rat studies has been used to tax top-down attention, the voluntary cognitive control functions used to modulate behavior in the face of challenge or changing reward contingencies (Posner & Snyder, 1975; Schiffrin & Schneider, 1977; see Gill et al., 2000; Himmelheber et al., 2000; McGaughy, Kaiser, & Sarter, 1996 for previous rat studies using this manipulation). For both species, we compared patterns of performance under normal conditions and after the introduction of a challenging distractor in the form of flashing background illumination. Maintaining performance in the face of attentional challenges is particularly dependent on increases in prefrontal cholinergic activity (Gill et al., 2000; Kozak, Bruno, & Sarter, 2006). For the human experiments, we also examined how performance changed in response to changes in reward contingencies, a manipulation that likewise requires top-down, voluntarily-controlled processes rather than lower-level perceptual or stimulus-driven (bottom-up) regulation of attentional systems (Sarter et al., 2006). Taken together, our results show that rats and humans show similar — though not identical — performance on the standard sustained attention task and similar responses to distraction, supporting the use of this task in translational research.¹

Experiment 1: Effects of Distraction on Sustained Attention in Rats and Humans

Method

General Procedures—Our main question was whether the demand to sustain attention over time and in the face of distraction resulted in similar patterns of performance for rats and humans. Both species performed a version of a sustained-attention signal-detection task (Figure 1; McGaughy & Sarter, 1995) under standard and distracting conditions. For each trial, participants indicated the presence or absence of a small, variable-duration stimulus presented

¹It is important to note that the central question in cross-species task validation is *qualitative*, not quantitative, similarity in responses to manipulations of construct-related variables. Although quantitative similarity has an intuitive, superficial appeal in terms of face validity, it would in fact be quite surprising if humans, who presumably have greater top-down control abilities, were not more robust than rats when dealing with challenges to such control. The criterion of qualitative rather than quantitative cross-species similarity has been used successfully both in the development of nonhuman primate versions of the CANTAB (e.g., Dias, Robbins, & Roberts, 1996; Roberts, Robbins, & Everitt, 1988; Weed et al., 1999) and a recent translation of human memory tests of familiarity and recollection to rodents (Fortin, Wright, & Eichenbaum, 2004; Sauvage, Fortin, Owens, Yonelinas, & Eichenbaum, 2008). See also Olincy and Stevens (2007) for a short review of the use of the prepulse inhibition task in humans and mice.

under either standard (constant lighting) or distracting (flashing houselight for rats, flashing computer screen for humans) conditions, with rewards for correct performance.

The long trial blocks, varied signal durations, and varied inter-trial intervals (ITI) employed in this task require participants to sustain high levels of attention in order to maintain successful performance (Bushnell et al., 2003; McGaughy & Sarter, 1995; Parasuraman & Mouloua, 1987). Distraction further challenges attention and performance (Gill et al., 2000; Sarter et al., 2006). Our primary prediction was that distraction would reduce accuracy as a function of signal duration and block of trials for both species. We also explored whether other factors that might influence attentional challenge such as event rate and the length of distractor presentation influenced standard task performance and interacted with distraction effects.

Experiment 1A: Sustained Attention in Rats—This experiment used the rat sustained-attention task described and validated by McGaughy & Sarter (1995) and used extensively to test acetylcholine's role in supporting sustained attention and performance in the face of attentional challenges (e.g., Kozak et al., 2006; McGaughy & Sarter, 1998). This experiment most closely follows the version used by Gill et al. (2000), Himmelheber et al. (2000), and McGaughy et al. (1996) in using the presence or absence of a flashing-houselight distractor as the major manipulation of challenge. An additional feature of this experiment is that we varied the number of blocks during which the distractor was presented to ask how distractor-related impairments might change over time: Does performance recover as the animal adapts, perhaps by increasing top-down control, further decline as a result of fatigue, or remain relatively stable?

Animals and animal housing: The subjects were 11 male Wistar rats (Harlan Sprague-Dawley, Indianapolis, IN) weighing 300-350 g at beginning of behavioral training. Animals were individually housed in a temperature- (23 °C) and humidity-controlled (45%) environment on a 12 h light/dark cycle (lights on at 7:00 a.m.). Animals were extensively handled prior to the beginning of training so that handling during experimental procedures would not lead to increased arousal. Food was available *ad libitum* (Rodent Chow, Harlan Teklad, Madison, WI). Water was provided as a reward for successful task performance (described below). Access to water was otherwise restricted to an 8-min period following daily operant training. Animal care and experimentation were performed in accordance with protocols approved by the University of Michigan's University Committee on Use and Care of Animals (UCUCA).

Apparatus: Behavioral training and testing was conducted in operant chambers (Med-Associates, St Albans, VT), located inside larger sound-attenuating chambers. Each operant chamber was equipped with an intelligence panel consisting of three panel lights (2.8 W), two retractable levers and a water dispenser (40-45 µL of water per delivery). A houselight (2.8 W) was located on the rear wall. Signal presentation, lever operation, reinforcement delivery and data collection were controlled by a Pentium PC and Med-PC for Windows software (V 4.1.3; Med-Associates).

Behavioral training procedures: The task, training method, and performance measures have been previously validated with respect to sustained attention (McGaughy & Sarter, 1995), and are briefly outlined.

The first step was to familiarize animals with the equipment and methods for obtaining reward. Animals were initially shaped to lever-press in accordance with a modified fixed-ratio schedule (each lever press was rewarded) for water reinforcement. Following at least three consecutive runs of >100 reinforced lever presses, animals began the first stage of training on the sustained attention task per se. During this stage, the houselight was turned off to increase the salience

of the signal, which consisted of a one-second illumination of the central panel light. Animals were trained to discriminate between the presence (signal event) or absence (nonsignal event) of this stimulus on each trial. Two seconds after the occurrence of each signal or nonsignal event, both levers were extended into the operant chamber. Responses were reinforced when one lever was pressed on signal trials (hits) and the other lever pressed on nonsignal trials (correct rejections). Incorrect lever presses (miss or false alarm errors) were not reinforced. If no response occurred within 4 s, the levers were retracted and an omission was recorded. The intertrial interval (ITI) was 12 ± 3 s. Intertrial interval, trial type (signal or non-signal) and signal duration were presented in a pseudo-random order with an equal distribution across trials (81 trials total). Left-right assignments were counterbalanced across animals. At this stage of training, incorrect responses resulted in up to three correction trials, in which the trial was repeated if the animal did not give a correct response. Continued incorrect responses resulted in a forced-choice trial, where only the correct lever was extended for 90 s or until a response was made. Correction and forced-choice trials aid in acquisition of response rules and help prevent development of a side bias (McGaughy et al., 1996).

Testing continued under these conditions until performance was stable, defined as at least three consecutive days in which performance reached a criterion of $\geq 60\%$ correct responses to both signal and non-signal events and $< 20\%$ omissions. The next stage introduced multiple signal durations (25, 50, 500 ms), shortened the ITI to 9 ± 3 s, and discontinued the correction and forced-choice trials. Following at least 3 days of criterion performance under these conditions, the houselights were illuminated throughout the task. This important modification requires the animals to constrain their behavior and presumably to maintain persistent orientation towards the intelligence panel.

After animals' performance stabilized at criterion for at least three consecutive days with the houselight illuminated, the next stage set the task length to 40 minutes, the duration to be used during data collection. Task runs were divided into five 8-min blocks. Animals were trained on the sustained attention task under standard conditions (houselight constantly illuminated) until reaching criterion performance levels for three consecutive runs. Animals were then trained under the distractor condition to familiarize them with the flashing (on/off at 0.5 Hz) houselight. Animals were first exposed to the distractor condition present in blocks 2 and 3 out of the 5 task blocks ("short" distractor condition). The distractor condition ran continuously throughout the blocks it was presented in. Animals next returned to testing under standard conditions until performance was at criterion for two consecutive days. They were then exposed to the distractor condition presented continuously through blocks 2-5 ("long" distractor condition). This "long" distractor condition differs only from the "short" distractor condition in the number of blocks distraction is present. Exposure to the distractor condition was again followed by standard testing for two days or until performance reached criterion.

Testing procedures: Upon completion of all training stages animals were tested on the full version of the sustained attention task (5 consecutive 8-minute task blocks) under standard conditions, with the short distractor, and with the long distractor. Only one condition was tested each day. Order of the distractor conditions (short, long) was counterbalanced across subjects. In between the distractor conditions, rats performed the task under standard conditions for two days or until performance was at criterion for two consecutive days. Data used for performance in the standard task were measured by averaging performance on the day prior to each of the two distractor conditions.

Experiment 1B: Sustained Attention in Humans—College students were tested in a conceptual replication of the rat experiment described above. The procedures used with humans differ from those used with rats in that they do not require extensive pre-training and are completed within a single session (see similar procedures by Bushnell et al., 2003; Mar, Smith,

& Sarter, 1996). However, they preserve the critical features of standard and distractor-condition testing, varying signal durations and ITIs, and reward for correct performance.

Participants: Sixteen participants (12 females, mean age = 19.7 years) were recruited through the introductory psychology subject pool and paid subject pools at the University of Michigan. All participants were right-handed as determined by the Edinburgh Handedness Scale (Oldfield, 1971), scored at least a nine on the Extended Range Vocabulary Test (ERVT; Version 3, Educational Testing Service (ETS), 1976; mean score = 16.9), had normal or corrected-to-normal vision, and had no conditions affecting attention or memory. The vocabulary test was used to screen out participants who might have had difficulty understanding the instructions or who were unmotivated or uncooperative. Participants were financially compensated or received course credit for their participation. They also received a small financial reward for performance on correct trials, analogous to the water reward used for rats. Participant recruitment and experimental procedures were in accordance with protocols approved by the University of Michigan's Behavioral Sciences Institutional Review Board.

Apparatus and procedures: A Dell PC with E-Prime software (Psychology Software Tools) was used for stimulus presentation and data acquisition. The standard "silver" color in E-prime was used as the static background for the standard condition, and the screen alternated between silver and black at 10 Hz for the distractor condition. The signal consisted of a small (3.5 mm²) gray square in the center of the screen. Headphones were used to present auditory cues and feedback; participants' responses were collected using the standard keyboard.

Participants were familiarized with task instructions and trained on the sustained attention task under standard conditions for 30 s and under distractor conditions for 30 s. Participants repeated practice until they reached $\geq 60\%$ accuracy on the standard condition practice.

Testing procedures: Participants completed four 10-minute runs of the sustained attention task. Task parameters were chosen on the basis of limited previous human work on this task (Mar et al., 1996) and pilot testing. Each experimental run consisted of 5 blocks of 2 minutes each. The four runs were a slow event-rate run (ITI = 6 ± 3 s) with all blocks in standard conditions, a fast event-rate (ITI = 2 ± 1 s) run with all blocks in standard condition, a fast event-rate run with block 2 in the distractor condition ("short" distractor), and a fast event-rate run with blocks 2 and 3 in the distractor condition ("long" distractor). The distractor stimulus ran continuously throughout the blocks it was presented. As for rats, the "short" and "long" distractor condition differ only in the number of blocks distraction is present. Run order was counterbalanced across participants.

The structure of individual trials was similar to that used for the rat experiment. Participants were required to detect a signal (small gray square) of varying durations (17, 50, or 100 ms) and to discriminate between signal and nonsignal events. One hundred milliseconds after the occurrence of a signal or nonsignal event, the response period was cued by a 75 ms low-frequency buzzer. Parallel to the rat experiment, responses were reinforced for pressing one key for signal trials and the other key for nonsignal trials ('z' key for left-hand responses; '/' key for right-hand responses, left-right assignments to signal or nonsignal trials counterbalanced across participants). Participants received one cent for every percentage point of overall accuracy for each run (\$1 maximum per run). A 75 ms high-frequency feedback tone followed correct responses, indicating to the participant that this trial would contribute to the performance-dependent financial reward. No feedback was given following incorrect trials or omissions (failures to respond within 1 s after the response buzzer). Within each run ITI, trial type (signal or nonsignal), and signal duration were varied in a pseudo-random order with an equal distribution across trials.

Data Analysis—Responses were recorded as hits, misses, correct rejections, false alarms, and omissions. The primary dependent measure used for subsequent analysis was the vigilance index (VI), which reflects performance across both signal and nonsignal trials. VI is used rather than the sensitivity index (SI; (Frey & Colliver, 1973)) because unlike SI, it is not confounded by errors of omission. It is calculated for each signal duration using the formula $VI = (\text{hits} - \text{false alarms}) / [2(\text{hits} + \text{false alarms}) - (\text{hits} + \text{false alarms})^2]$. VI varies from +1.0 to -1.0, with +1 indicating that all recorded responses were hits or correct rejections and -1 indicating all recorded responses were misses or false alarms (see tables for detailed hit and false alarm data).

The design of this experiment potentially allows the analysis of a relatively large number of effects and interactions. To reduce the number of Type I errors, our analyses were limited to our central questions about the effects of distraction and signal duration. For example, ITI was varied within each run so that trials appeared unpredictably, thus increasing the demands on attention, but ITI level was not a variable of primary theoretical interest and is not included as an independent variable. In addition, for the human experiments we varied the ITI between the two standard runs (2 ± 1 s vs. 6 ± 3 s) to examine whether this manipulation had any effect on this condition (Bushnell et al., 2003; Parasuraman & Mouloua, 1987). However, this comparison did not indicate reliable effects or interactions. Thus, for humans, repeated-measures ANOVAs were conducted on the standard and distractor conditions that used the 2 ± 1 s ITI. The independent variables were Run (standard, short-distractor, and long-distractor conditions), Block, and Signal Duration. For each experiment, we first report the results of the 3-way interaction tests, followed by simpler tests targeted at our questions about distraction and signal duration. Separate repeated-measures ANOVAs were conducted on omissions.

We also conducted signal detection analyses (Swets, Tanner, & Birdall, 1961) to better assess the effects of our variables on perceptual sensitivity (d') and bias (B''_D), with the latter presumably more influenced by top-down, voluntary control processes. d' sensitivity measures were calculated from the proportions of hits and of false alarms, P_H and P_{FA} for each stimulus duration using the formula: $d' = z(P_H) - z(P_{FA})$ (Green & Swets, 1966). Data from short- and long-distractor runs were combined within no-distractor and distractor blocks to calculate P_H and P_{FA} for each subject. For d' measures, the effective limit (with $P_H = 0.99$ and $P_{FA} = 0.01$) is 4.65 and d' is zero when $P_H = P_{FA}$. B''_D measures of bias were calculated using the formula $B''_D = [(1-P_H)(1-P_{FA}) - P_H P_{FA}] / [(1-P_H)(1-P_{FA}) + P_H P_{FA}]$ (Donaldson, 1992). B''_D scales from -1 to +1, with negative numbers indicating a liberal bias, positive numbers indicating a conservative bias, and zero indicating no bias. Both measures were analyzed using repeated-measures ANOVAs with the independent variables Distraction (no-distraction, distraction) and Signal Duration, followed by simpler tests to investigate distraction effects within each signal duration.

For all analyses, the Huyhn-Feldt sphericity correction was applied as needed. Corrected F and p values are reported, but degrees of freedom are rounded to integer values for easier reading. For repeated measures ANOVAs, effect sizes were computed using generalized eta squared (η^2_G , Olejnik & Algina, 2003). Bakeman (2005) suggested for η^2 sizes 0.02 as small, 0.13 as medium, and 0.26 as large, similar to η^2 guidelines (Cohen, 1988). For t -tests, effect sizes were reported using Cohen's d , with corrections for repeated measures (Cohen, 1988).

Experiment 1: Results and Discussion

Our main question was how overall performance, as indicated by the vigilance index (VI), varied across conditions for rats and for humans (Figure 2). As described above, analyses were restricted to the standard, short-distractor, and long-distractor runs with the same ITI parameters. The 3-way Run X Block X Duration interaction was not statistically significant for the rat experiment, ($F(16, 160) = 1.00, p = 0.45, \eta^2_G = 0.03$), but was significant within the

human experiment ($F(16, 240) = 4.47$, $p < 0.0001$, $\eta^2_G = 0.06$). As we elaborate on below, the major differences between the species were that rats showed lower performance overall, with distractor-related declines at all durations and difficulty recovering performance after distraction, whereas humans showed very high performance overall and only had statistically significant effects of the distractor at the shortest signal duration.

Omissions were generally low in both species (for rats, $2.47 \pm 1.07\%$ of trials per run; for humans, $1.61 \pm 0.55\%$ of trials per run) and did not differ significantly across experimental conditions, $F < 1.00$ for both species.

Performance without Distraction is Signal Duration-Dependent—Performance (VI) on the standard task was duration-dependent for both rats ($F(2,20) = 54.35$, $p < 0.0001$, $\eta^2_G = 0.45$) and humans ($F(2,30) = 4.45$, $p = 0.03$, $\eta^2_G = 0.04$), with better performance at longer durations (Figure 2, see Tables 1 and 2 for hit and false alarm data that go into the calculation of VI). Mere time on task did not influence performance for either species, as indicated by the lack of a Block main effect or significant Block X Duration interaction for either rats or humans, all $F \leq 1.00$.

Distraction Impairs Task Performance—The Run X Block interaction comparing performance (VI) across blocks for the standard, short-distractor, and long-distractor runs was significant (both $p < 0.001$) for both rats and humans, indicating that the distractor impaired performance for both species (Figure 2). The Block x Duration interaction was not significant for rats, $F(8,80) = 1.31$, $p = 0.25$, $\eta^2_G = 0.01$, but was for humans, $F(8,120) = 7.76$, $p < 0.0001$, $\eta^2_G = 0.05$. Subsequent analyses looked within each distractor run to compare the results for those blocks during which the distractor was present versus those during which it was not.

In simple analyses comparing all no-distractor blocks with all distractor blocks, distraction reduced performance for both rats and humans in both the short- and long-distractor runs. (Rat short-distractor run, $t(10) = 3.79$, $p < 0.01$, Cohen's $d = 1.20$, long-distractor run, $t(10) = 4.02$, $p < 0.01$, Cohen's $d = 1.73$; human short-distractor run, $t(15) = 2.83$, $p = 0.01$, Cohen's $d = 0.88$, long-distractor run, $t(15) = 4.13$, $p < 0.005$, Cohen's $d = 1.16$). Inspection of Figure 2 suggests that the main differences between the species were that rats had low performance overall, with floor effects in some distraction cells ($VI \sim 0$), and also had difficulty recovering performance after distraction. When the rats' distractor blocks were compared only to the first no-distractor block in each run, they showed marginal Block x Duration effects for the short-distractor run, $p = 0.06$ and $\eta^2_G = 0.08$, paralleling the results found for humans. However, VI was not significantly different from zero (chance performance) in all distraction cells for the short distractor, and in all cells for the long distractor except for VI 500 in blocks 2 and 4 and VI 50 in block 5 (all $p < 0.05$ and Cohen's $d > 0.78$). For the short-distractor run the first no-distractor block following distraction (block 4) was significantly lower than the first block in the run ($p = 0.04$, Cohen's $d = 1.04$) and not different from the distractor blocks (all $p > 0.10$, Cohen's $d < 0.69$). For all but the shortest duration, performance began to recover by the second post-distractor block, and was intermediate. Similar floor effects at shorter signal durations following an attentional challenge were previously reported on this task in rats (e.g., McGaughy et al., 1996; Kozak et al., 2006), suggesting the 500 ms duration may be the most useful to examine when considering manipulations that decrease hit accuracy.

Humans showed higher performance overall, smaller distraction effects that were only statistically significant at the shortest duration, and had near-immediate, full recovery after exposure to the distractor. The Block X Duration interaction was significant for both distractor runs (both $p < 0.0001$). Analyses at each Duration level showed that for the 17 ms condition, VI was significantly lower for distractor blocks than no-distractor blocks in both distractor runs, both $p < 0.005$, $\eta^2_G = 0.36$ for the short-distractor condition, and $\eta^2_G = 0.30$ for the long-

distractor condition. In contrast, the distraction effect was not statistically significant for the two longer durations, all $p > 0.07$, although performance was numerically worse in the distractor condition even for these durations. (For the short-distractor run, $\eta^2_G = 0.07$ for the 50 ms duration and $\eta^2_G = 0.03$ for the 100 ms duration. For the long-distractor run, $\eta^2_G = 0.08$ for the 50 ms duration and $\eta^2_G = 0.11$ for the 100 ms duration.) Humans did not show significant differences between pre-distractor and post-distractor blocks, all $p > 0.20$.

Distraction effects on perceptual sensitivity (d') and response bias (B)—Signal detection analyses were performed to better understand the performance of both species. In particular, we were interested in the degree to which performance drops in the distraction condition were related to a loss of perceptual sensitivity and in potential species difference in response criterion (c.f., Bushnell et al., 2003).

For rats, the d' measure in the distraction condition at the shortest signal duration was near zero, consistent with the impression of floor performance in this condition given by the VI analyses (Figure 3). For the other two durations, performance in the distraction condition was low but significantly above zero (both $p < 0.005$). By contrast, humans' d' was significantly above zero for all conditions, including the shortest duration under distraction conditions, Figure 3, all $p < 0.0001$). Further, while post-hoc analyses of humans' VI (above) found significant distraction effects within only the shortest duration, post-hoc tests on their d' results showed significant effects of distraction within both the 17 ms and the 50 ms signal durations (both $p < 0.05$, $\eta^2_G > 0.08$). This suggests that especially in the longer-duration conditions, humans may have been able to use top-down attentional control to partially counteract the perceptual difficulties imposed by distraction. For both species, all other effects for the d' measure were in the expected direction, with significant effects of Distraction, Duration, and their interaction, all $p < 0.01$.

We also calculated measures of response bias (B''_D) for both species. For rats, both misses and false alarms increased under distraction, $p < 0.001$ and $\eta^2_G > 0.15$ for the short- and long-distractor runs. However, for humans, misses were sensitive to distraction for each of the distractor runs, $p < 0.005$, $\eta^2_G > 0.11$, but false alarms were only marginally affected, $p > 0.05$, $\eta^2_G > 0.06$. This difference suggested rats and humans had different criterion shifts in response to the uncertainty introduced by distraction, a suggestion borne out by analysis of the B''_D measure (Figure 4).

The signal detection analyses revealed that rats had a more conservative response bias overall, but shifted towards a more liberal criterion when distraction introduced uncertainty. Of interest, duration and distraction had opposite effects: Shortened duration led to a more conservative response bias ($F(2,20) = 41.70$, $p < 0.0001$, $\eta^2_G = 0.01$), whereas distraction led to a more liberal response bias, ($F(1,10) = 4.85$, $p = 0.05$, $\eta^2_G = 0.07$). Humans showed very little response bias at the two longer durations, consistent with their overall high performance in these conditions. In keeping with the effects of duration found in rats, humans also showed a shift towards a more conservative response criterion in the shortest duration. However, distraction in the short-duration condition had the opposite effect on humans than it did in rats, leading to a more conservative, rather than a more liberal, response bias (Figure 4).

In summary, our results showed fundamental similarities between rat and human performance both in the standard task and in the two species' response to distractor challenge, but we also found important differences that were likely due to humans' greater capacity for top-down control. The strongest similarities were seen in the standard, no-distractor condition: both species showed better performance for longer signal durations, and neither species' performance was influenced by mere time-on-task. Both species showed performance declines in the face of distraction, although these effects were more evident in rats than in humans with

the sample sizes and stimulus parameters used here. In part because of the floor effects and slow recovery post-distraction on the two shorter durations in rats, across species the pattern of distraction effects are most similar when comparing rats' performance at 500 ms duration to humans' performance at 17 ms. The signal detection analyses revealed that distraction similarly reduced perceptual sensitivity for both species. In contrast, rats and humans responded somewhat differently in their (presumably top-down) shifts in response criterion. Both species responded to shorter durations by becoming more conservative, but rats became more liberal in the face of distraction, whereas humans showed the opposite effect.

To better understand the effects of distraction on human performance and the influence of top-down control processes on their response to distraction, we conducted a second experiment using only human participants. This experiment used a larger sample size, to test whether the numerical effects of distraction seen at the longer durations (Figure 2, bottom panel) would be significant with greater power. More importantly, it changed the reward contingencies to encourage a shift towards a more liberal response criterion. Specifically, an increased penalty was imposed for "miss" responses, with the expectation that this would increase the probability of false alarms and lead to a more liberal response bias under conditions of uncertainty.

Experiment 2: Top-down Manipulation of Sustained Attention Task Performance in Humans

Method

General Procedures—Procedures were identical to Experiment 1B except that the reward contingencies for performance-based payment were changed to penalize misses. Thirty-two participants (19 females, mean age = 18.7 years, mean Extended Range Vocabulary Test score = 18.7) were instructed that they would be monetarily penalized 5 cents for each percentage point of misses for every run. This penalty was subtracted from the 1 cent per percentage point correct payment the subjects earned on each run.

Our primary prediction for this experiment was that, relative to Experiment 1B, participants would show fewer misses and more false alarms if performance on this task was sensitive to top-down manipulation. In line with this shift towards more false alarms, we also predicted participants in this experiment would have a more liberal response bias than participants in Experiment 1B. Finally, the large number of misses relative to false alarms during distraction in Experiment 1B raises a potential concern about the source of the errors (problems perceiving the stimuli versus top-down biases to respond negatively under conditions of uncertainty). Changes in the error distributions and in the response bias measures between Experiment 1B and 2 would support the role of top-down biases in generating the error data seen in Experiment 1B.

Data Analysis—Analysis of data followed the procedures outlined for the animal experiment and the first human experiment. To examine the error data between this experiment (Experiment 2) and the prior human experiment (Experiment 1B), a 3-way ANOVA was conducted with Error Type (false alarms, misses) and Distraction (no distraction, distraction) as within-subject factors, and Experiment (E1B, E2) as a between-subject factor. As in the first experiment, analyses focused on the three runs (standard, short-distractor, long-distractor) with similar ITIs.

Experiment 2: Results and Discussion

For VI, the 3-way Run X Block X Duration interaction was significant, $F(16,496) = 3.92$, $p < 0.001$, $\eta^2_G = 0.02$. Errors of omissions were generally low ($2.50 \pm 0.53\%$ of trials per run) and

did not differ significantly across experimental conditions ($F(2,62) = 1.23, p = 0.30, \eta^2_G < 0.01$).

Replication of Experiment 1B Effects: Duration and Distraction Influence

Performance—Performance (VI) in the standard, no-distractor condition replicated the effects found in Experiment 1B (Figure 5; see Table 3 for hits and false alarms). Performance was better for longer durations than for shorter ones, $F(2,62) = 13.70, p < 0.0001, \eta^2_G = 0.04$, and remained stable across the five task blocks.

Also replicating the previous experiment, distraction again impaired performance. Collapsing across durations, distractor blocks showed significantly lower VI values than no-distraction blocks for the short- and long-distractor runs, both $p < 0.05$ (Figure 5). The Duration X Block interaction was also statistically significant, $F(8,248) = 3.72, p < 0.01, \eta^2_G = 0.04$ for the short-distractor condition and $F(8,248) = 7.79, p < 0.0001, \eta^2_G = 0.04$ for the long-distractor condition, with larger distraction effects for the shorter durations. However, the greater power of this experiment revealed significant distraction effects for all durations, not just the shortest one. For the long-distractor run, the distractor effect was statistically significant within every signal duration, all $p < 0.05$ and $\eta^2_G > 0.08$. For the short-distractor run, the distraction effect was statistically significant for the 17 ms and 100 ms durations, both $p < 0.05, \eta^2_G = 0.16$ for 17 ms duration and $\eta^2_G = 0.06$ for the 100 ms duration, and marginal for the 50 ms duration, $F(4,124) = 2.45, p = 0.06, \eta^2_G = 0.05$. These effect sizes are very similar to the ones found in E1B ($\eta^2_G = .03 - .11$), suggesting that our failure to detect statistically significant distraction effects at the longer durations in Experiment 1B were the result of insufficient power.

Similarly to the previous human experiment, analysis of d' sensitivity measures found a significant Distraction by Duration interaction ($F(2,62) = 13.44, p < 0.0001, \eta^2_G = 0.04$). The main effects of Distraction and Duration were likewise significant (both $p < 0.0005, \eta^2_G \geq 0.12$), as in the previous experiment. In line with the distraction effects described for VI, sensitivity measures revealed distraction effects at all three signal durations. Within each duration, sensitivity measures were significantly lower during distraction than without distraction for each of the three signal durations (all $p < 0.05$, Figure 3).

Performance is Sensitive to Top-Down Manipulations—Besides the increased sample size, the major difference between the current experiment and E1B was the 5-cent penalty for misses. In Experiment 1B, most errors were misses, with very few false alarms. This could occur either because participants had primarily bottom-up difficulties in perceiving the signal stimulus, particularly under distracting conditions, or because of a top-down bias to respond negatively when distraction increased uncertainty. If the results were due to bias, a shift in the reward contingencies should lead to a shift in how people responded under uncertain conditions and a different distribution of error types.

The shift in reward contingencies indeed resulted in a shift in error distribution, consistent with manipulations of top-down control processes (Figure 6). A 3-way ANOVA comparing Experiment (1B, 2), Distraction (no-distractor, distraction), and Error Type (false alarms, misses) resulted in a significant 3-way interaction, $F(1,46) = 5.11, p = 0.03, \eta^2_G = 0.01$. Importantly, the main effect of Experiment was not significant, $p > 0.60$, indicating that the two experiments did not differ in the overall amount of errors, only in their distribution. Simpler analyses to probe the interaction revealed that there were no significant differences between the two experiments in the no-distractor condition, $F(1,46) = 0.32, p = 0.58, \eta^2_G < 0.01$. Instead, the effects of reward contingency were most evident in the distraction condition: In Experiment 1B, distraction primarily increased the number of misses ($F(1,15) = 12.01, p < 0.005, \eta^2_G = 0.15$), but the increase in false alarms was marginal ($p = 0.06, \eta^2_G = 0.10$). By

contrast, in E2, the proportion of misses and false alarms were almost equal under distraction ($F(1,31) = 0.32, p = 0.58, \eta^2_G = 0.002$).

The signal-detection analyses for this experiment also supported the idea that the types of errors seen in E1B (mostly misses) were attributable to top-down biases in how to respond under conditions of uncertainty, rather than simply difficulty perceiving the signal stimulus during distraction. A 3-way ANOVA comparing Experiment (1B, 2), Distraction (no-distraction, distraction), and Duration (17 ms, 50 ms, 100 ms) found no effects of Experiment on d' sensitivity measures. In contrast, the Distraction X Experiment interaction was statistically significant for the B''_D bias measure, $F(1,46) = 8.90, p < 0.005, \eta^2_G = 0.03$. In particular, whereas in E1B distraction led to a more conservative response bias for humans within the shortest signal duration, in E2 it led to a more liberal response bias, an effect paralleling the results found for rats (E1A, see Figure 4).

General Discussion

Although animal models play a critical role in developing treatments for various neuropsychological disorders, the degree to which an experimental task measures similar cognitive functions across species has been rarely determined. The present experiments address that issue, with a particular focus on manipulations thought to invoke voluntary or “top-down” modulation of attentional performance. These functions are of interest because they are thought to rely on frontal-parietal circuits, to be mediated by the function of the cholinergic system and, if disrupted, to contribute to the cognitive symptoms disruptions in a variety of neuropsychiatric disorders, including schizophrenia (e.g., Mar et al., 1996; Sarter, Nelson, & Bruno, 2005).

Our results generally support the view that tasks developed for animal research can be effectively re-designed for research in humans, while also revealing important differences apparently related to humans’ greater top-down control. Both species maintained performance over time in the standard condition, showed reduced performance at shorter durations compared to longer durations, and also showed reduced performance under distracting conditions. These patterns partially replicate the findings of Bushnell and colleagues (2003), in that they find generally similar performance in the task overall and in response to manipulations of signal strength (signal intensity in their study, signal duration in ours). However, we did not find support for gender² and species differences in the effects of trial rate, although this may have been due to our particular stimulus parameters and a failure to find strong effects of trial rate overall.

The signal detection analyses provided important insights as to potential species differences in top-down control versus bottom-up perceptual processes, particularly in response to the distraction manipulation.³ Although humans had greater sensitivity overall, both species showed a reduction in sensitivity (d') in response to reduced signal duration and in response to distraction. As would be expected, this measure of perceptual sensitivity was not affected by the manipulation of reward contingency. The bias or response-criterion measures showed quite different effects, revealing interesting distinctions in both species’ reactions to different

²Gender analyses were conducted in human experiment (E2) to investigate whether the gender differences found by Bushnell et al. (2003) were replicated here; no consistent effects of gender were found. Evaluation of the effects of gender is limited by the relatively low number of subjects (13 males in E2) and is not possible here in rats (all males used).

³Bushnell et al. (2003) informally suggested that their human participants might have a more conservative response bias than did rats. However, this suggestion was based on the species differences in false alarm rates; formal signal-detection analyses were not conducted. Inspection of their data shows that the two species did not significantly differ in terms of hits. A simpler way to summarize the results of the two experiments might be to say that regardless of hit rates, humans generally produce very low false alarm rates when different error types are equally penalized.

sources of uncertainty. Both rats and humans responded to reduced signal intensity by becoming more conservative. However, they responded quite differently to distraction: Rats adopted a more liberal response criterion under distracting conditions. In contrast, humans became more conservative when distraction was introduced, with a large drop in hits accompanied by only a small increase in false alarms. However, a change in reward contingencies that penalized misses led humans to show a performance pattern much more like that of the rats, with a generally more liberal response criterion under distraction conditions than under the standard conditions. Taken together, the d' and bias measures suggest that both species show similar bottom-up effects of changes in signal strength (duration) and distraction, and that both respond to these effects by exercising top-down control processes — albeit in somewhat different directions. Importantly, prior work suggests response bias and responsivity to positive or negative feedback may differ in clinical populations such as Parkinson's (e.g., Frank, Seeberger, & O'Reilly, 2004), amnesia (e.g., Yonelinas, Kroll, Dobbins, Lazzara, & Knight, 1998) or in aging (e.g., Marschner et al., 2005; Samanez-Larken et al., 2006). Thus, in addition to basic variables like signal duration, the effects of manipulating reward contingencies may need to be separately reexamined in populations outside the normal young adult population used here.

This brings us to the larger point that the experiments reported here are the first, not the last, steps in the development and validation of this task for cross-species and patient research. As described earlier, the usual criterion for such task validation is qualitative (not quantitative) similarity across species (c.f., Weed et al., 1999; Sauvage et al. 2008). Inherent species differences in perception, motivation, and top-down control make it difficult to obtain quantitative matches without extreme manipulations. For example, Bushnell et al. (2003) used a three-times longer signal duration and 42-times larger stimulus range for rats as compared to humans in order to roughly equate mean performance between rats and humans. In the present paper, for the rat task we used stimulus parameters common to previous studies using this task in rats (Himmelheber et al., 2000; Kozak et al., 2006, McGaughy & Sarter 1995); for the human studies we used stimulus parameters based on a paper exploring a somewhat different version of this task in humans (Mar et al., 1996) and on our own pilot testing. These parameters were chosen to facilitate the comparison of the present results with the relevant literature. It is of some interest that overall performance and the effects of distraction (in terms of both the basic VI measure and the effects on d') are similar for the rats in the 500 ms condition and humans in the 17 ms condition. However, rather than attempting to quantitatively match rat and human performance (which would likely rely on increasing stimulus durations for rats rather than further reducing them for humans, given the already low values for the former species), a more useful direction would be to establish the stimulus parameters and reward contingencies that would avoid floor and ceiling effects and allow the full examination of performance within each species.

The cross-species performance differences that exist are most likely due to differences in top-down control and task constraints. It is also possible that perceptual differences between the species influence performance, although previous work suggests that rats do not fare any better on an auditory version of the task (e.g., Turchi & Sarter, 1997). The most obvious differences related to task constraints and top-down control are that humans can be explicitly instructed, require less extensive training, and are seated in front of a computer screen with little else to do — it is unlikely that they will miss a signal because they happen to be engaged in grooming behavior. That said, rats have a very low rate of omissions (which would indicate inattention to the task) and maintain this low rate even during distraction, suggesting that they remain highly motivated and engaged with the task. It is possible that even the standard task requires a reasonable degree of top-down control in rats, whereas in humans it may be largely driven by bottom-up processes. If so, the difficulty rats show in recovering performance after distraction could reflect these greater demands on top-down control resources. Another

possibility, not exclusive with differences in the standard task, is that continued performance in the face of distraction is more exhausting of top-down control resources for the rats. The difference in post-distractor recovery is the most prominent qualitative difference between the species, and will require further exploration. (For example, if human performance in the standard condition is largely a function of bottom-up, stimulus-driven attention, performance in the distractor condition but not the standard condition should be affected by other demands on top-down control, such as cross-modal distraction or a verbal shadowing task.)

These questions of motivation, perception, and top-down control will also need to be considered when adapting the task for use with patient populations who may also differ from normal controls on these variables. For example, in patient research it may be useful to select a range of stimulus durations that allows good performance by both patients and controls in the standard version of the task, and then test whether distraction differentially impacts the performance of these two groups. Other critical steps for task validation and development will be tests of psychometric properties (e.g., test-retest reliability, correlations with other measures of attention and top-down control to further establish construct validity), and examination of the neural substrates of standard and distractor-task performance in humans to see how well they correspond to the predictions made from the neurobiological examinations of this task in rats. These experiments are underway (e.g., Demeter, Sarter, & Lustig, 2007).

In summary, the goal of the present experiments was to examine the feasibility of translating the rat-based distractor-condition version of a sustained attention task into a version that can be used in humans. This was done by testing the hypothesis that both species would show qualitatively similar responses to the manipulation of variables related to the constructs of interest, in this case sustained attention and top-down control. The results are quite promising: Rats and humans show largely similar patterns of performance both in the standard task and in response to manipulations of distraction and other stimulus variables. In particular, both showed reduced accuracy, perceptual sensitivity and changes in top-down bias under conditions of shortened duration or increased distraction, although the direction of top-down responses to the distraction manipulation were somewhat different. Further testing will be needed to better understand the differences that remain between the species, to establish the psychometric properties of the test, and to determine the task parameters that will be most useful for different patient populations or drug research. The present paper lays the groundwork for such experiments, and for studies examining the neuronal mechanisms underlying genetic variation in attentional performance (e.g., Kim et al., 2006). Although cross-species translational work imposes considerable challenges, it also holds great promise for better understanding the specific neurotransmitter systems underlying attention-network activations seen in human neuroimaging studies and refining animal models of human cognition in both healthy and disordered groups.

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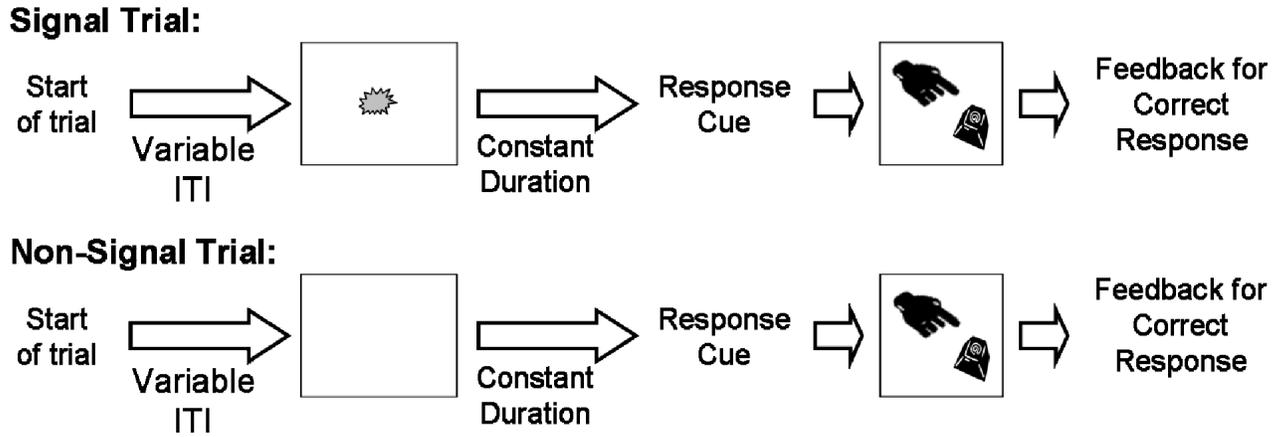


Figure 1. Schematic of sustained attention task used for rats and humans. Each trial began with a variable delay separating it from the previous trial (intertrial interval, ITI), after which a brief light stimulus either appeared (signal event) or did not appear (nonsignal event) in the center of the display. Signal and non-signal events were pseudo-randomized with 50% trials of each type. After a short, constant delay, participants were then cued to indicate whether a signal had or had not occurred on that trial. Correct responses (both hits and correct rejections) were rewarded (water reward for rats, feedback tone signaling a monetary reward for humans); incorrect responses and omissions did not receive any feedback.

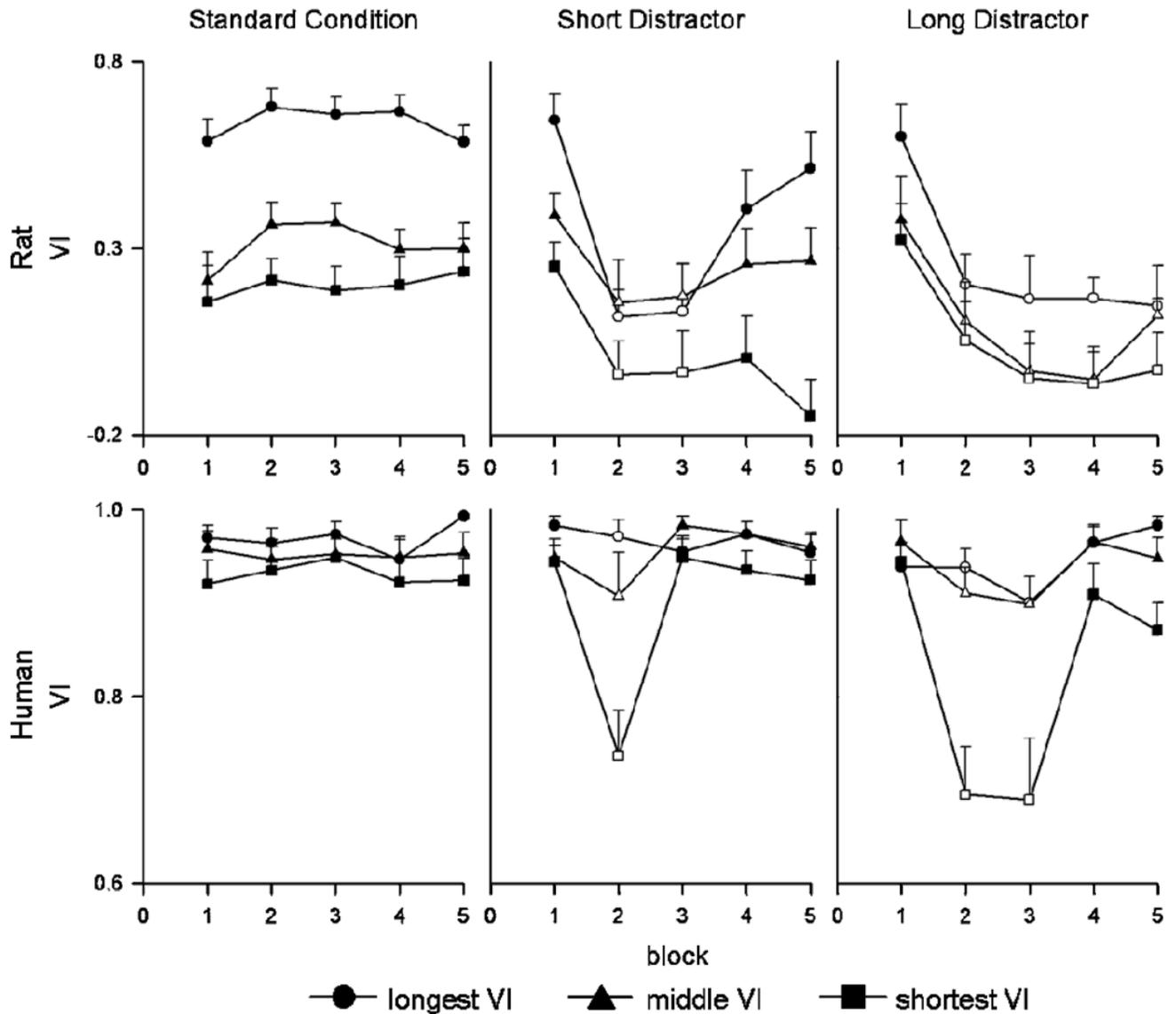


Figure 2.

Both species are influenced by stimulus duration and distraction. Each graph shows the mean vigilance index (VI; see text for calculation) across blocks and distraction conditions for the three different run types. Rat data are in the top panels, human data in the bottom panels. The leftmost panel shows data from the no-distractor run, the middle panel shows data from the run with only a short period of distraction (2 blocks for rats, 1 block for humans), the right panel shows data from the run with a longer period of distraction (4 blocks for rats, 2 blocks for humans). Solid symbols indicate a block with no distraction; hollow symbols indicate a block with distraction. Symbol shape indicates whether the signal was presented for a short, middle, or long duration (25, 50, or 500 ms for rats; 17, 50, or 100 ms for humans). Both species show substantial effects of signal duration even in the standard, no-distractor condition (leftmost panels and solid symbols in all panels). Neither species showed performance declines as a function of mere time on task. Rats showed substantial performance declines in the face of distraction at all durations, whereas for humans the effects of distraction were most pronounced at the shortest signal duration. (See text for statistical details.)

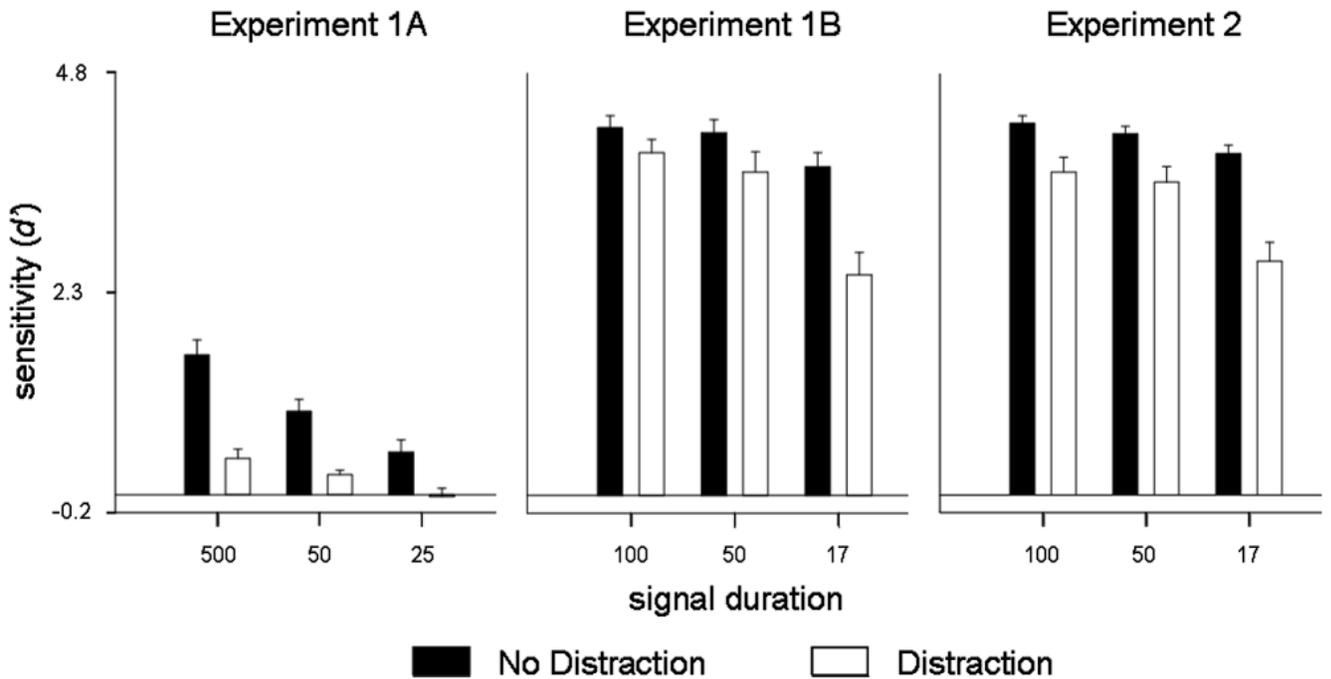


Figure 3. d' sensitivity measures for rats (Experiment 1A) and humans (Experiment 1B and 2). Bars represent the sensitivity measures from the no-distractor (black bars) and distractor (white bars) blocks combined across the short- and long-distractor runs. Error bars represent standard error around the mean. Both species show a reduction in sensitivity as a result of shortened signal duration and distraction, although these effects are more pronounced for rats than for humans. Supporting the conclusions drawn from the VI results, the rats show lower sensitivity overall and are at floor in the lowest signal duration. Changes in reward contingency for humans did not affect the d' sensitivity measures (compare E1B and 2).

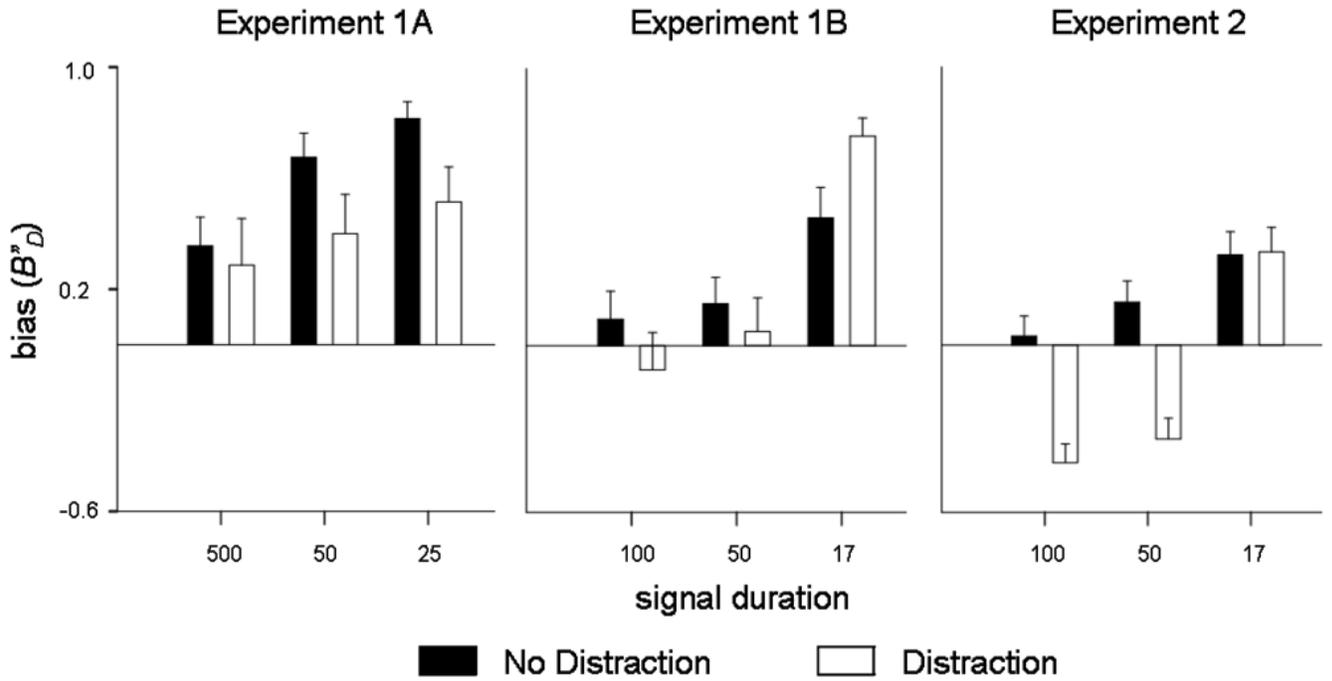


Figure 4. Bias measures for rats (Experiment 1A) and humans (Experiment 1B and 2). Bars represent the bias measures from the no-distractor (black bars) and distractor (white bars) blocks combined across the short- and long-distractor runs. Error bars represent standard error around the mean. Both species show an increasingly conservative bias in response to reduced signal duration. However, rats show a more conservative bias overall and a liberal shift in response to distraction. E1B: Humans show the opposite response to distraction in the shortest duration, adopting a very conservative response bias. E2: When misses are penalized, humans tend to adopt a liberal response criterion under distraction, so that the effects of distraction on their bias measures resemble the effects on rats (E1A).

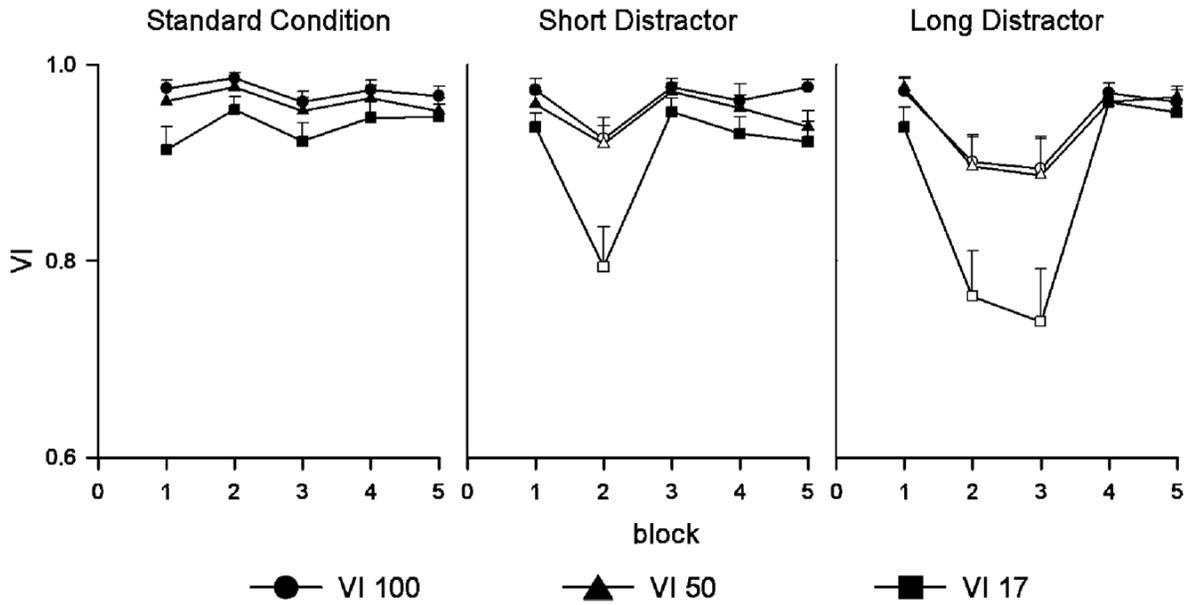


Figure 5.

E2: Overall human attentional performance (VI) when misses are penalized is similar to performance under equal reward contingencies (compare to Figure 2). Data shown are from Experiment 2, in which misses were penalized more than false alarms. As in Figure 2, black symbols indicate the no-distractor condition whereas white signals indicate the presence of the distractor, and error bars represent standard error around the mean. These patterns generally replicate those seen in the first human experiment (Figure 2). The size of the distractor effects is generally similar across experiments (see text), but is significant for all durations in this experiment in part because of the increased sample size.

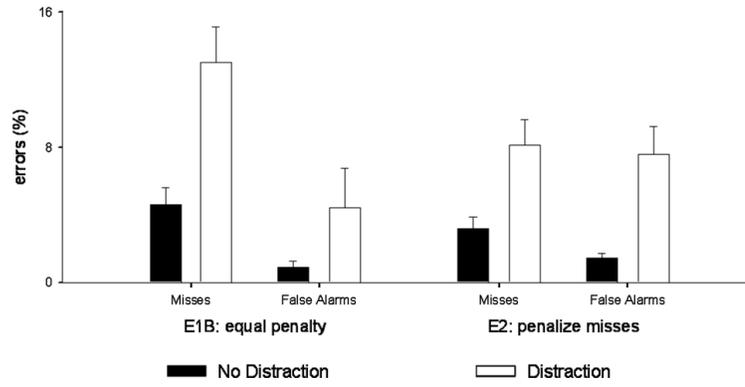


Figure 6.

Changes in reward contingencies to penalize misses reduce misses and increase false alarms under distracting conditions. Bars represent the error data from E1B (equal penalties) and E2 (misses penalized), collapsed across short- and long-distractor runs. Error bars represent standard error around the mean.

Table 1
E1A: Hits and false alarm percentages for sustained attention task in rats
 Data are means (standard error around the mean). Distraction is present in blocks 2 and 3 of the short-distractor condition and in blocks 2-5 of the long-distractor condition, indicated with italics.

Block	Hits to 500 ms signal	Hits to 50 ms signal	Hits to 25 ms signal	False alarms
Standard Condition				
1	78.2 (5.2)	42.4 (5.7)	37.4 (6.3)	21.6 (2.5)
2	83.4 (4.5)	51.6 (4.8)	35.0 (4.3)	16.8 (1.3)
3	81.8 (5.0)	52.2 (6.5)	35.4 (6.0)	19.7 (2.5)
4	82.4 (3.7)	44.4 (6.1)	35.4 (4.1)	19.3 (2.8)
5	74.6 (4.5)	48.4 (5.3)	42.8 (5.1)	20.1 (2.7)
Short-Distractor Condition				
1	78.8 (7.3)	51.3 (6.1)	37.6 (5.0)	17.4 (2.6)
2	<i>55.3 (6.4)</i>	<i>56.8 (9.2)</i>	<i>44.9 (6.8)</i>	<i>46.8 (5.6)</i>
3	<i>45.4 (9.2)</i>	<i>41.4 (6.8)</i>	<i>24.6 (4.7)</i>	<i>28.0 (5.3)</i>
4	49.1 (6.8)	32.2 (6.3)	18.7 (4.9)	10.6 (1.4)
5	69.3 (6.3)	41.6 (5.8)	14.3 (4.5)	20.4 (6.6)
Long-Distractor Condition				
1	77.9 (5.9)	54.4 (9.7)	46.3 (8.6)	19.2 (4.1)
2	<i>61.6 (7.0)</i>	<i>56.0 (8.9)</i>	<i>48.6 (8.4)</i>	<i>45.6 (6.8)</i>
3	<i>43.6 (10.8)</i>	<i>30.6 (9.0)</i>	<i>26.4 (7.2)</i>	<i>27.6 (5.7)</i>
4	<i>44.9 (7.4)</i>	<i>26.0 (5.1)</i>	<i>28.2 (6.9)</i>	<i>28.6 (4.2)</i>
5	<i>42.4 (8.6)</i>	<i>34.6 (4.7)</i>	<i>26.6 (6.0)</i>	<i>24.6 (4.1)</i>

Table 2
E1B: Hits and false alarm percentages for sustained attention task in humans
 Data are means (standard error around the mean). Distraction is present in block 2 of the short-distractor condition and in blocks 2-3 of the long-distractor condition, indicated with italics.

Block	Hits to 100 ms signal	Hits to 50 ms signal	Hits to 17 ms signal	False alarms
Standard Condition				
1	97.9 (1.4)	96.6 (1.8)	91.6 (3.4)	1.1 (0.6)
2	93.4 (1.8)	95.8 (1.9)	93.1 (3.9)	1.4 (0.8)
3	97.9 (1.4)	95.6 (2.0)	94.8 (2.5)	0.8 (0.5)
4	96.3 (2.0)	96.8 (1.7)	93.7 (2.6)	2.2 (1.0)
5	100.0 (0.0)	95.8 (1.9)	91.6 (3.0)	0.8 (0.8)
Short Distractor Condition				
1	98.9 (1.1)	94.8 (2.5)	94.5 (2.1)	0.8 (0.5)
2	<i>100.0 (0.0)</i>	<i>93.6 (3.0)</i>	<i>69.9 (5.9)</i>	<i>3.6 (2.4)</i>
3	95.8 (1.9)	98.9 (1.1)	94.8 (2.5)	0.8 (0.5)
4	97.8 (1.4)	97.9 (1.4)	93.6 (2.1)	0.8 (0.5)
5	95.8 (2.4)	96.8 (1.7)	92.4 (2.7)	1.1 (0.6)
Long Distractor Condition				
1	93.7 (2.6)	96.9 (2.3)	94.7 (2.0)	0.8 (0.5)
2	<i>98.9 (1.1)</i>	<i>95.8 (2.4)</i>	<i>68.8 (5.9)</i>	<i>6.3 (2.9)</i>
3	<i>92.6 (2.6)</i>	<i>92.6 (2.6)</i>	<i>68.1 (6.8)</i>	<i>3.4 (1.2)</i>
4	97.9 (1.4)	97.9 (1.4)	90.7 (3.7)	1.5 (0.7)
5	98.9 (1.1)	94.8 (2.5)	85.4 (3.3)	0.8 (0.5)

Table 3
E2: Hits and false alarm percentages for the penalized misses experiment in humans

Data are means (standard error around the mean). Distraction is present in block 2 of the short-distractor condition and in blocks 2-3 of the long-distractor condition, indicated with italics.

Block	Hits to 100 ms signal	Hits to 50 ms signal	Hits to 17 ms signal	False alarms
Standard Condition				
1	100.0 (0.0)	98.4 (1.1)	93.1 (2.1)	2.6 (0.9)
2	100.0 (0.0)	98.9 (0.7)	96.2 (1.5)	1.4 (0.6)
3	97.9 (1.0)	96.8 (1.4)	93.2 (2.0)	2.0 (0.6)
4	97.9 (1.0)	96.8(1.4)	94.5 (1.8)	0.7 (0.4)
5	98.3 (1.0)	96.6 (1.3)	95.8 (1.5)	1.7 (0.5)
Short Distractor Condition				
1	99.0 (1.0)	97.4 (1.3)	94.6 (1.6)	1.7 (0.5)
2	<i>97.9 (1.2)</i>	<i>97.2 (1.2)</i>	83.5 (3.6)	<i>6.1 (1.5)</i>
3	98.9 (0.7)	98.4 (0.9)	96.2 (1.3)	1.3 (0.5)
4	97.2 (1.5)	96.0 (1.6)	93.0 (2.0)	1.2 (0.5)
5	99.5 (0.5)	95.1 (1.4)	93.2 (2.0)	1.8 (0.6)
Long Distractor Condition				
1	98.3 (1.2)	98.8 (0.8)	94.1 (2.1)	1.5 (0.8)
2	<i>97.6 (1.2)</i>	<i>97.3 (1.4)</i>	<i>81.3 (4.1)</i>	8.9 (2.5)
3	<i>96.3 (1.4)</i>	<i>96.0 (1.6)</i>	78.7 (3.7)	7.7 (2.4)
4	98.4 (0.9)	97.3 (1.1)	97.3 (1.1)	1.6 (0.7)
5	96.8 (1.4)	97.4 (1.3)	95.8 (1.3)	1.1 (0.4)