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Ordinal Judgments in the Rat: An Understanding of Longer and Shorter for Suprasecond, but Not Subsecond, Durations

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Ordinal Judgments in the Rat: An Understanding of *Longer* and *Shorter* for Suprasecond, but Not Subsecond, Durations

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An emerging corpus of clinical and neuroimaging data suggests that subsecond and suprasecond durations are represented via 2 distinct mechanisms in humans; however, surprisingly, behavioral data to this effect are lacking. In our first experiment, we perform the first systematic exploration of subsecond and suprasecond timing within the same session in nonhuman subjects. Rats were trained to judge the relative duration of 2 sequential stimuli, responding on one lever if the first stimulus was *longer* or on a second lever if the converse was true. Our data provide strong evidence of an abstract understanding of *longer* and *shorter* for durations in the suprasecond range, whereas responding was at chance levels for durations in the subsecond range. Data from a second experiment reveal that this pattern is not due to an inability to time subsecond signals, as rats respond systematically in subsecond and suprasecond bisection tasks. Together, our results provide the first clear behavioral evidence of a discontinuity in the mental time line. These data from rats are discussed in light of similar findings of a discontinuity in the mental number line in human infants.

Keywords: interval timing, cerebellar timing, ordinality, time perception

A growing corpus of data demonstrates primitive timing abilities in a diverse range of non-human animal species, from zebrafish and mice to pigeons and monkeys (e.g., Buhusi et al., 2009; Cheng, Jesuthasan, & Penney, 2011; Fetterman, 2006; Pleil, Cordes, Meck, & Williams, 2011; Zarco, Merchant, Prado, & Mendez, 2009). Studies reveal that animals discriminate stimuli based upon their duration (e.g., Meck & Church, 1983; Roberts, 1995; Ross & Santi, 2000) and systematically time a stimulus to anticipate delivery of a reward (e.g., Cordes & Gallistel, 2008). Remarkably, animal timing data show striking similarities to those collected with human participants (across development—infants, children, and adults) in that discriminations obey Weber's law; that is, the ease with which two values are discriminated is based upon their ratio, not their absolute difference (e.g., Allman, Pelphrey, & Meck, 2012; Brannon, Libertus, Meck, & Woldorff, 2008; Brannon, Suanda, & Libertus, 2007; Droit-Volet, Clement, & Fayol, 2008; Droit-Volet, Meck, & Penney, 2007; Meck & Church, 1983; Rakitin et al., 1998; vanMarle & Wynn, 2006). These behavioral findings have led researchers to conclude that all species share a system for representing time that must have arisen early in evolutionary history and is present early in development (Gallistel, 1990).

Timing data from clinical populations, imaging studies of typical adults, and lesion studies with non-human animals, however, suggest that more than one cognitive mechanism may be responsible for representing temporal durations. Specifically, subsecond and suprasecond timing often appear to be modulated by two distinct neural substrates, resulting in distinct timing dissociations if focally impaired (e.g., Breukelaar & Dalrymple-Alford, 1999; Buhusi & Cordes, 2011; Buhusi & Meck, 2005; Ivry & Keele, 1989; Koch et al., 2008, 2007; Lewis & Miall, 2003a, 2003b—but see Teki, Grube, & Griffiths, 2012, for an alternative view). For example, when repetitive transcranial magnetic stimulation (rTMS) is delivered over the lateral cerebellum, adults overestimate subsecond durations, whereas suprasecond timing is relatively spared, and the reverse pattern is found for rTMS over the right dorsolateral prefrontal cortex (Koch et al., 2007). The same is true for cerebellar lesions in rats—they appear to selectively impair subsecond but not suprasecond timing (Breukelaar & Dalrymple-Alford, 1999). Furthermore, some studies have shown that, under certain conditions, individuals with Parkinson's disease (PD) show impaired suprasecond, but not subsecond timing (Koch et al., 2008—but see Allman & Meck, 2012, and Merchant, Harrington, & Meck, in press, for an alternative view). In a recent comprehensive, voxel-wise meta-analysis of neuroimaging studies involving timing tasks, subsecond timing was found to activate a distinct set of cortical networks from that of suprasecond timing (Wiener, Turkeltaub, & Coslett, 2010). Similar findings were obtained from a voxel-based analysis of patients with various lesions (Gooch, Wiener, Hamilton, & Coslett, 2011). Based on these studies as well as findings revealing that suprasecond, but not subsecond timing, is impaired by high cognitive load (Rammsayer & Lima, 1991; although see Rammsayer & Ulrich, 2005, for counter-evidence), it has been suggested that there are two distinct timing mechanisms—an automatic, mechanism for processing of

durations in the millisecond range and a more cognitively controlled mechanism for the processing of longer durations in the suprasecond range (Lewis & Miall, 2003a, 2003b).

Despite this clinical and neurobiological evidence for a two-system model of timing, behavioral data to this effect is lacking. In fact, behavioral timing studies generally treat subsecond and suprasecond timing as one and the same because data from these two ranges reveal very similar behavioral patterns (e.g., Droit-Volet, 2008; Droit-Volet, Tourret, & Wearden, 2004; Melgire et al., 2005). Importantly, however, these studies compare data from distinct tasks and/or experimental sessions—subsecond and suprasecond durations are rarely interspersed within the same timing task (e.g., Droit-Volet & Wearden, 2002; Himpel et al., 2009; Mangels, Ivry, & Shimizu, 1998)—making a direct comparison of performance across these two timing ranges inexact. Moreover, in the case of non-human subjects, subsecond and suprasecond timing data are not only collected in distinct tasks, but in distinct sessions interrupted by an intervening training period during which the subject is trained on a new set of stimulus response rules, thus providing confounds to both psychophysical and neurobiological examinations of the mental time line (e.g., Breukelaar & Dalrymple-Alford, 1999). Thus, behavioral data supporting the existence of two distinct timing mechanisms may be lacking due to experimental design limitations. Critically, to truly explore the question of these distinct timing mechanisms at both the behavioral and neurobiological levels in non-human animals, tasks requiring subsecond and suprasecond timing within the same session are necessary.

An ordinal-comparison task, in which animals learn an ordinal rule for responding that can be applied across a wide range of temporal durations, is just such a task that can open the door for investigations of these distinct timing mechanisms (Gu & Meck, 2011). Whereas discrimination studies reveal that non-human animals and preverbal infants understand that 2 s is *different from* 8 s, ordinal tasks explore whether they understand that 2 s is *shorter than* 8 s, or that 200 ms is *shorter than* 800 ms, and so on. Whereas in standard discrimination tasks, animals judge the absolute duration of a single signal, in contrast, in ordinal tasks, animals experience *two* distinct signals (e.g., a white noise and a tone) and are trained to respond based upon the *relative* duration of the two signals. Importantly, this relative response rule can then be applied across the timeline, allowing for an exploration of timing abilities across both subsecond and suprasecond durations.

Although many studies have explored appreciations of *numerical* ordering in both non-human animals and preverbal human infants (e.g., Addessi, Mancini, Crescimbene, Pado-Schioppa, & Visalberghi, 2008; Agrillo, Dadda, Serena, & Bisazza, 2008; Brannon, 2002; Brannon & Terrace, 1998; Cantlon & Brannon, 2006; Carazo, Font, Forteza-Behrendt, & Desfilis, 2009; Hauser, Carey, & Hauser, 2000; Irie-Sugimoto, Kobayashi, Sato, & Hasgawa, 2009; Jaakkola, Fellner, Erb, Rodriguez, & Guarino, 2005; Suanda, Tompson, & Brannon, 2008; see Anderson & Cordes, 2013, for review), only a few studies, primarily with pigeons, have demonstrated nonverbal comprehension of an abstract ordinal rule for temporal quantities (i.e., durations; Dreyfus, Fetterman, Smith, & Stubbs, 1988; Fetterman, 2006; Fetterman & Dreyfus, 1986; Van Rooyen & Santi, 2009).[1] In these studies, pigeons experience the successive presentation of two visual stimuli that vary in duration and are trained to respond on two choice keys based upon the relative duration of the two stimuli. For example, animals may be trained to respond on one key if the duration of the first stimulus was longer and the other key if the second stimulus was longer. Recently, a similar paradigm was adopted with rats as well (Santi, Hoover, & Simmons, 2011). Data from these tasks reveal that both pigeons and rats perform above chance in this task, with response accuracy varying as a function of the ratio of the two durations to be tested, suggesting that these animals are able to engage in abstract temporal ordering (Cordes, Williams, & Meck, 2007). However, there are still open questions regarding the extent of these nonverbal ordinal abilities.

In particular, although this ordinal task has been used to explore non-human temporal ordinal abilities across a wide range of values, no studies have systematically characterized these abilities across the time continuum, specifically comparing performance on subsecond (<1 s) and suprasecond (>1 s) durations. In light of evidence suggesting subsecond and suprasecond timing are regulated via two distinct neurobiological mechanisms, such an investigation is needed. To address this gap in the temporal integration literature, in our first experiment, rats were trained to respond based upon an ordinal rule, in which correct responding required the rats to take into account the durations of two distinct auditory/visual stimuli and compare their durations. These data add to the growing evidence that non-human animals appreciate the inherent ordinal nature of abstract temporal durations. In addition, importantly, rats were tested on a broad range of durations, ranging from as short as 100 ms up to 22 s, allowing for the first systematic examination of non-human animal timing abilities across both the subsecond timing range (durations <1 s) and the suprasecond timing range within the same experimental sessions, opening the door to explore questions regarding the continuity of the mental time line. Evidence suggests rats were able to generalize this ordinal rule to suprasecond, but not subsecond, durations. In a second experiment, a second group of rats was placed in standard subsecond and suprasecond duration bisection tasks in order to characterize rat temporal discrimination abilities in these distinct timing ranges.

Experiment 1

Method

Subjects. Subjects were eight experimentally-naïve male Sprague-Dawley rats approximately 5 months of age at the beginning of the experiment. Rats were housed in pairs in a temperature-controlled room, under a 12 hr light/12 hr dark (LD) cycle. Rats were provided free access to water in their home cages and were maintained at 85% of their ad lib weight by restricting access to food. Experiments were conducted in accordance with standard procedures approved by the Institutional Animal Care and Use Committee at Duke University.

Apparatus. The apparatus consisted of eight standard lever boxes (Model ENV-007, MED Associates, Inc., Albans, VT)

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[1] Although some have suggested that the temporal bisection task, in which rats are trained to discriminate between two standard durations (e.g., 2 and 8 s) and then presented with intermediate durations (e.g., 4 s; Meck & Church, 1983), is a test of ordinal understanding, these tasks are by their very nature similarity judgments and do not provide a formal test of ordinal understanding (see Cordes, Williams, & Meck, 2007; Meck, 1997).

housed in light and sound attenuating cubicles (Model ENV-019, MED Associates, Albans, VT). Each lever box was equipped with two response levers situated on the front wall of the box on either side of a food cup, attached to a pellet dispenser (45 mg precision food pellets, Research Diets, Inc. New Brunswick, NJ). On the wall above each lever were three LED lights (one red, one yellow, and one green, Model ENV-222M, MED Associates, Albans, VT). A noise amplifier/speaker system was installed in each box, mounted on the opposite wall from the levers. A Windows XP (Microsoft, Redmond, WA) based computer system running MED-PC Version IV Research Control & Data Acquisition System software (Med Associates, St. Albans, VT) attached to an electronic interface was used to control the experimental equipment and record the data. All auditory stimuli were presented at a volume of 88 dB above background.

Procedure. Experimental sessions were conducted at approximately the same time each day for 1 hr during the light phase of the LD cycle.

Magazine and lever training. Rats first received combined magazine and lever training. During each session, one food pellet was dispensed automatically once each minute, and in addition, every lever press produced a pellet. One lever was extended into the chamber at a time until 10 presses were made (producing 10 food pellets) and the lever retracted, and the other lever was extended until 10 reinforced presses were made. When all rats lever-pressed at least 100 times within the session, they were transitioned to the ordinal task.

General procedure of ordinal task. Trials during the ordinal training and testing always proceeded as follows: A white noise signal was presented for a predetermined duration (X s) followed by a silent interstimulus interval (1.5 s). Then, both the tone (1,500 Hz) and LED lights [2] were turned on for a different predetermined duration (Y s). The computer program randomly determined the durations (X and Y) of the stimuli and whether the white noise (X) or tone + LED (Y) would be presented for the longer duration (X > Y or X < Y). Immediately after the tone and LED lights were extinguished, two levers were extended into the chamber and rats were then expected to press the lever corresponding to the stimulus presented for the "longer" duration. That is, correct responses on the right lever corresponded to when the duration of the white noise was "longer" than the duration of the tone (X > Y). Correct responses on the left lever corresponded to trials in which the tone was "longer" (Y > X). Immediately following a correct response, rats received a food pellet, and the levers were retracted, ending the trial. Incorrect responses or a failure to respond within 8 s resulted in retraction of the levers and termination of the trial without a reward. The next trial began following a variable intertrial interval (ITI—exponentially distributed with E(60)). On average, rats experienced 49.6 (range 38–68) trials per session.

Training on ordinal task. Following magazine and lever training, rats were placed in ordinal training. Initially, rats were placed in the full ordinal task (trials tested all possible duration combinations) in which on 50% of the trials, only the correct lever was extended into the chamber. Following 30 sessions, responding failed to exceed chance levels. Thus training proceeded in blocked sessions where rats were trained to discriminate a single duration pairing across several sessions involving exclusively choice trials (2 levers extended into the chamber). To begin blocked training, rats were first trained to discriminate 1 s from 5 s in this ordinal

task. Thus, on every trial, the computer randomly determined which of the two stimuli (white noise or tone + LED) would be presented for 1 s and which would be presented for 5 s. Training on 1 s versus 5 s proceeded until responding by all rats exceeded chance levels (50%) for 3 consecutive days (31 sessions). In the same manner, rats were then exclusively trained on a 0.5 s versus 2.5 s discrimination (8 sessions) and then exclusively trained in a 2.5 s versus 12.5 s discrimination (5 sessions). Once performance exceeded chance in all of these discriminations, all three duration pairings were randomly presented across trials in the same experimental sessions (6 sessions) prior to commencement of ordinal testing.

Ordinal testing. Following blocked training on the ordinal task, rats were placed in ordinal testing for 18 sessions. On every trial, one stimulus (white noise OR tone + LED) was presented for a Standard duration (.4, .7, 1.2, 2.0, 3.0, or 5.5 s), and the other stimulus was presented for a Comparison duration (a 1.4-, 1.8-, 2.3-, or 4-fold [3] change shorter or longer than the Standard; see Table 1 for all duration pairs presented). On every trial, the computer randomly determined whether the first signal (white noise) would be presented for the Standard or Comparison duration and whether the Comparison duration would be longer or shorter than the Standard. Thus, there were 60 different Standard-Comparison duration pairings that could be presented to the rat (6 (Standard durations) × 5 (Comparison ratios) × 2 (Comparison shorter or longer than Standard) = 60). Importantly, correct responding on this task required attention to the durations of both stimuli and the ability to make an ordinal comparison. Neither the duration of either individual signal (white noise OR tone + LED) nor the total duration of sound was sufficient to produce correct responding on the task.

Data analysis. Data from the 18 ordinal test sessions are analyzed here. All trials with a response time longer than 3 standard deviations away from the mean response time for each individual rat and trials with no response within the 8-s limit were discarded (accounting for an average of 2% of all trials across rats).

Results and Discussion

Rats succeeded in learning an ordinal response rule, performing significantly above chance (50%) on the task ($M = 62.5\%$, $t(7) = 9.7$, $p < .0001$, Cohen's $d = 3.55$). This was the case for all eight rats, in that the number of correct responses out of the total number of trials for each rat was significantly greater than chance (Binomial Statistic, all ps < 0.0001), confirming that rats responded based upon a quantitative rule requiring the comparison of the durations of two distinct signals. Not only did rats perform better than chance across the 18 test sessions, but they did so immedi-

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[2] Note, the second signal was composed of a compound auditory/visual stimulus (tone plus LED lights) so as to maximize the discriminability of the two signals.

[3] On a few rare trials (due to a programming error in the first few test sessions), the comparison duration was 5-fold longer or shorter than the standard duration. Due to the rarity of these trials, and because these trials were equally distributed as longer than or shorter than the standard, these trials were combined with the 4-fold comparison data. Thus, the 4-fold comparison trials encompassed all data at the outer-endpoints of the distributions.

Table 1

All Comparison and Standard Pairings Used in Experiment 1 (in Seconds)

Standard duration	.4	.7	1.2	2.0	3.0	5.5
/4	.1	.18	.3	.5	.75	1.38
/3	.13	.23	.4	.66	.99	1.82
/2.3	.18	.31	.53	.88	1.32	2.42
/1.8	.22	.39	.66	1.1	1.65	3.03
/1.4	.28	.5	.85	1.42	2.13	3.91
×1.4	.56	.98	1.68	2.8	4.2	7.7
×1.8	.72	1.26	2.16	3.6	5.4	9.9
×2.3	.92	1.61	2.76	4.6	6.9	12.7
×3	1.2	2.1	3.6	6	9	16.5
×4	1.6	2.8	4.8	8	12	22

ately. Performance during the first 50 trials of testing on the very first ordinal test session was also significantly above chance levels ($M = 60.5\%$, $t(7) = 3.5$, $p < .01$, $d = 1.23$). Given that rats were tested on as many as 60 different Standard-Comparison duration pairings throughout each test session, it would have been impossible to determine the probability of reinforcement for each of these pairings during these initial 50 trials, suggesting that performance cannot be explained entirely by sensitivity to reward probabilities.

In addition to above-chance responding, data revealed systematic patterns of responding as a function of the ratio of the durations of the comparison to the standard signals. Percentage correct scores were subjected to a 6 (standard values) × 10 (comparison ratios) repeated measures analysis of variance (ANOVA) that revealed a significant main effect of comparison ratio ($F(9, 315) = 11.5$ $p < .0001$, partial $\eta^2 = .62$), a main effect of Standard ($F(5, 315) = 27.4$, $p < .0001$, partial $\eta^2 = .80$), and a significant Standard × Comparison interaction ($F(45, 315) = 2.7$, $p < .0001$, partial $\eta^2 = .28$). The main effect of Comparison ratio reflected the fact that performance generally adhered to Weber's law (see Figure 1). Much like responding in other timing tasks with both humans and other animals, the probability of a correct response increased as a function of the ratio between the Comparison and

Standard durations, such that performance was worse when the ratio between the two values approached 1.0. Further analyses confirmed this finding. Regressions relating the probability of a "Comparison longer than Standard" response to the ratio between the Comparison and Standard (averaging across all standards) revealed positive slopes for all eight rats (Binomial statistic, $p < .001$), and as a group, the slopes were significantly greater than zero, $t(7) = 37.8$, $p < .0001$, $d = 13.36$. Thus, data suggest that the probability of a correct response was dependent upon the ratio of the two durations in the trial, consistent with Weber's law.

Adherence to Weber's law, however, appeared to be dependent upon the range of values tested. A distinct pattern of responding was observed for judgments of subsecond and suprasecond durations. Whereas suprasecond timing appeared systematic and Weber-like, subsecond timing was not. This observation was supported by further results of the ANOVA. The main effect of Standard revealed that rats performed better as the duration of the standard increased (see Figure 2). This was the case for all eight rats—the slopes of the lines relating accuracy scores (averaged across all Comparison values) across Standard values were positive for all eight rats, $t(7) = 10.1$, $p < .0001$, $d = 3.57$; Binomial statistic, $p < .001$, indicating an increase in performance as the duration of the Standard value (and corresponding Comparison values) increased. In fact, analyses revealed that rats performed at chance levels for the shortest Standard value tested (400 ms; $M = 52\%$, $t(7) = 1.3$, $p > .2$, $d = .46$), but performed above chance levels for all the other Standard durations (all $ps < 0.01$). This suggests that although responding was ratio-dependent, it also improved significantly as a function of the absolute value of the durations tested.

Most importantly, both of these main effects were qualified by the significant Standard × Comparison interaction. This interaction reflected the fact that responding became more dependent upon the ratio of the Comparison to the Standard (and thus more orderly) as the duration of the Standard increased. As can be seen in Figure 3, when the tested durations were shorter than 1 s, responding was only slightly better than chance levels, whereas as soon as the stimuli were presented for longer than 1 s, data was
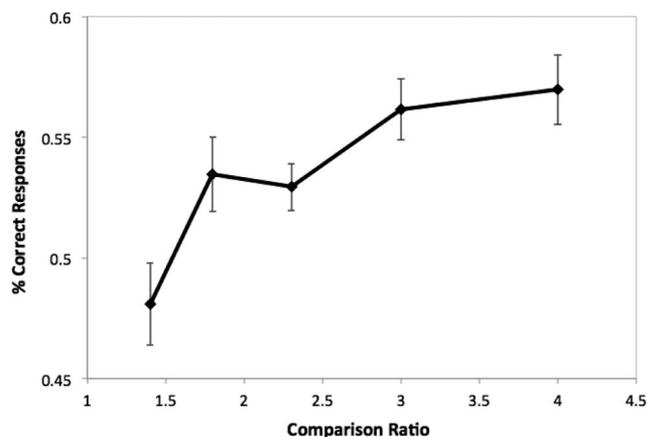

Figure 1. Percentage correct responses as a function of the ratio of the comparison to the standard for all eight rats. Error bars depict standard errors.
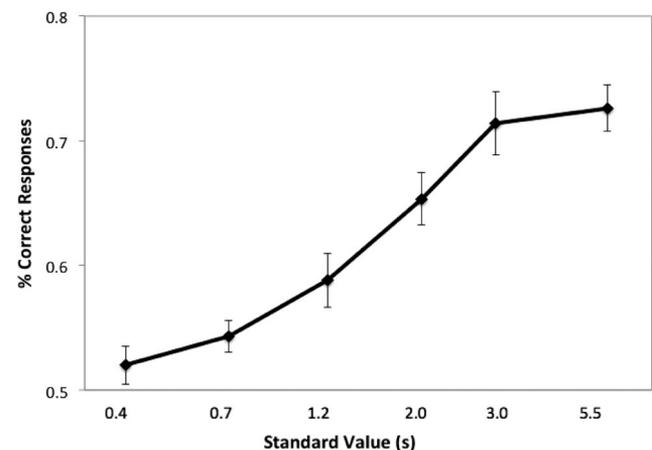

Figure 2. Accuracy in responding as a function of the standard duration (plotted on a log scale) for all eight rats. Error bars depict standard errors. s = second.
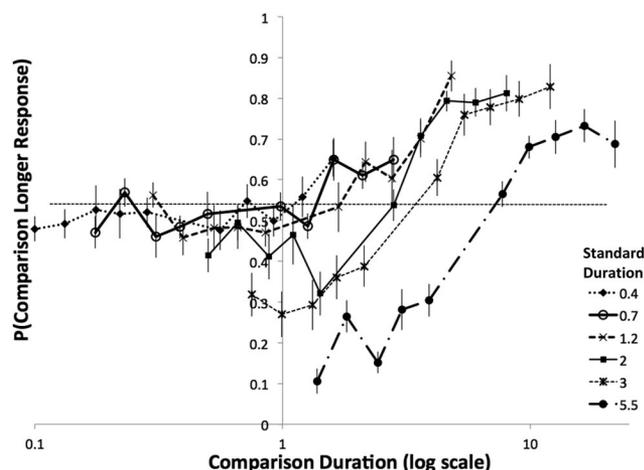
Figure 3. The probability of a response indicating the comparison duration was longer than the standard duration as a function of the comparison duration (plotted on a log scale) for all eight rats. Error bars depict standard errors. P = probability.

systematic and accurate, resembling normal psychometric functions. This pattern is suggestive of a break in the mental time line at 1 s, where rats were able to respond based upon ordinal relationships for durations within the interval timing range (>1 s), but failed to do so in the subsecond timing range (<1 s). This dissociation was confirmed by further statistics.[4] Regression analyses revealed that although the slopes of the lines relating the probability of a Comparison "longer" response to the Comparison duration increased as a function of the Standard durations for all eight rats (Binomial, $p < .001$; $t(7) = 7.7$, $p < .001$, $d = 2.7$), this occurred in a stepwise manner. That is, these slopes did not increase across Standards exclusively within the subsecond range (that is, there was no systematic increase in the slopes from the 400 ms standard to the 700 ms standard: $t(7) = 0.7$, $p > .05$, $d = .25$), nor across Standards exclusively within the suprasecond timing range (no systematic increase in the slopes across the 2, 3, and 5.5 s Standards: $t(7) = 1.4$, $p > .05$, $d = .51$).[5] Thus, these data suggest that although rats were able to learn the task and perform above chance levels, they treated durations in the subsecond range in a distinctly different fashion than durations in the suprasecond range, suggestive of a possible dissociation in the mental time line.

Experiment 2

Data from our ordinal task reveal that rats were unable to generalize an ordinal rule learned across suprasecond durations to the subsecond duration range. We suggest that data are indicative of a break in the mental time line, revealing that rats represent subsecond durations in a distinctly different manner than suprasecond durations, consistent with clinical and neurological data to this effect (e.g., Breukelaar & Dalrymple-Alford, 1999; Gooch et al., 2011; Koch et al., 2007). However, it is also possible that the chance-level responding observed for the shortest durations may be indicative of a general inability to discern subsecond durations. Although it is generally assumed that rodents, like humans, are capable of tracking durations across the time line, there is surprisingly little behavioral evidence to support this claim. Roger, Has-

broucq, Rabat, Vidal, and Burle (2009) recorded rat encephalographic responses to small temporal variations (mismatch negativity), and data revealed smooth discrimination functions for durations in the subsecond range (150 ms); however, it is unclear whether behavioral responses mimicked this pattern. Behavioral evidenced garnered from trace eye-blink conditioning tasks has revealed rats are sensitive to subsecond duration intervals (e.g., Weiss, Bouwmeester, Power, & Disterhoft, 1999); however, timing the onset of an aversive event may entail a distinctly different ability than making judgments about the duration of neutral sound stimuli. Furthermore, Breukelaar and Dalrymple-Alford (1999) reported systematic responding by rats in a subsecond time bisection task; however, this was following previous training on a suprasecond bisection task as well as after cerebellar or sham lesion surgeries, both of which could have influenced responding.

To verify that rats were able to represent subsecond durations in our ordinal task while also providing some of the first behavioral data to characterize subsecond timing abilities in intact rats, in our second experiment, a second group of naïve rats were trained on a subsecond duration temporal bisection task (modeled after Meck & Church, 1983). Rats were initially trained to discriminate a 300 ms from a 1,200 ms stimulus and then tested with intermediate probe durations (e.g., 540 ms). Following subsection bisection training and testing, the same rats were trained on a suprasecond duration bisection task (2 s vs. 8 s) in order to compare temporal discrimination abilities across the time line within the same subjects.

Method

Subjects. Subjects were eight experimentally naïve male Sprague Dawley rats (different from those of Experiment 1). All animal housing and feeding procedures were identical to that of Experiment 1. Unfortunately, during Day 11 of subsecond bisection testing, one of the rats needed to be removed from the experiment for health reasons. Because this rat participated in 10 days of testing, its data are included in all subsecond analyses. Furthermore, equipment failure resulted in the loss of data for one more rat during the suprasecond bisection testing. Thus, although subsecond bisection data analyses included data from eight rats, suprasecond task analyses only included data from a total of six rats.

Apparatus. The experimental chambers, apparatuses, and stimuli were the same as those used in Experiment 1.

Procedure.

Discrimination training. Rats were tested for 1.5-hr sessions at approximately the same time each day. Following magazine and lever training (identical to Experiment 1), rats were placed in a simple duration discrimination task in which they were trained to press one lever following a 300 ms signal and to press the other lever following a 1,200 ms signal. To ensure rats were able to time both stimuli used during our ordinal task, animals were first trained

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[4] Unfortunately, because responding in the subsecond range was relatively flat, curve-fitting of the data and follow-up likelihood analyses to determine if the data were best fit by one or multiple psychometric functions was impossible.

[5] Note, the 1.2 s standard was excluded from this analysis as it straddled the border between the subsecond and suprasecond timing ranges.

to discriminate white noise signals (22 sessions). Following consistent above-chance responding, the signals were switched to compound Tone + LED light signals (identical to Experiment 1; 29 sessions). All training and testing thereafter (including suprasecond bisection testing) used Tone + LED light compound signals.

Trials began with the onset of the signal. The signal lasted for either 300 ms or 1,200 ms (randomly determined by the computer on every trial). Once the duration elapsed and the signal extinguished, both levers extended into the chamber. Rats were trained that responses on one lever (e.g., the left lever) were reinforced (with a food pellet) following the short signal and responses on the other lever (e.g., the right lever) were reinforced following the long signal. Incorrect responses (e.g., responses on the right lever following a short signal) or no response within 8 s ended the trial without reinforcement. The side of the correct "long" lever was counterbalanced across subjects. For the first 5 sessions of either signal training, only one lever (the correct response) extended into the chamber on 50% of trials to promote acquisition. Once the trial ended, the next trial began following a variable ITI—exponentially distributed with E(60).

Subsecond probe testing. Following tone + LED signal discrimination training (29 sessions), rats experienced probe test sessions (15 sessions) in which on 40% of trials, the duration of the signal was one of six intermediate durations (370, 450, 540, 660, 810, or 980 ms). On these probe trials, responses to either lever were unreinforced. On the remaining 60% of trials, trials were identical to that of discrimination training. During subsecond training and testing, rats experienced an average of 81.9 trials per session (range 61–102).

Suprasecond bisection training and testing. Following subsecond bisection probe testing, rats were placed in suprasecond discrimination training in which they were trained to discriminate a 2-s tone + LED signal from an 8-s one (12 sessions). Again, once responding reached criterion levels, the rats were placed in test sessions (13 sessions) in which 40% of trials were unreinforced probe trials involving signals lasting an intermediate duration (2.4, 3.0, 3.6, 4.4, 5.4, or 6.6 s). During suprasecond bisection training and testing, rats experienced an average of 78.3 trials per session (range 67–93).

Data analyses. Data from subsecond and suprasecond testing phases were analyzed separately. The probability of the rat responding on the lever associated with the long signal (P(long)) was computed for each signal duration for each rat across all test sessions. Data from each rat was then fit via the method of maximum likelihood with a three-parameter sigmoid function $(y = \dfrac{a}{1+e^{-(t-c)b}}$, where a, b, and c were free parameters and t was the stimulus duration) to determine the point of subjective equality (PSE; the duration at which the probability of a "long" response was 50% - a measure of the location of the curve), the difference limen (DL; half of the difference between the duration at which P(long) = 0.75 and P(long) = 0.25 – a measure of the precision in the distribution of responding), and the Weber fraction (w; the ratio of the DL to the PSE—a normalized measure of response precision allowing for a comparison across subsecond and suprasecond duration data).

Results

Data from both the subsecond and suprasecond testing phases revealed a systematic pattern of responses, with the probability of a "long" response increasing as a function of the duration presented (see Figure 4). In addition to adding to the existing corpus of suprasecond bisection data from rodents, data also provide strong evidence to support claims that rodents are capable of discriminating auditory/visual stimuli presented for subsecond durations.

Analyses of the PSEs returned by sigmoid fits of the suprasecond and subsecond data revealed a different behavioral pattern across the two duration ranges. As has been reported previously with nonhuman animal subjects (e.g., Breukelaar & Dalrymple-Alford, 1999; Meck & Church, 1983), the suprasecond PSEs did not differ significantly from the geometric mean of the two anchor values (4 s; $M = 4.16$, $t(5) = 1.12$, $p > .3$, $d = .46$) and was significantly less than the arithmetic mean (5 s; $t(5) = 5.95$, $p < .002$, $d = 2.43$). In contrast, the PSEs for the subsecond data approximated the arithmetic mean (750 ms; $M = 725.4$; $t(7) = 1.56$, $p > .16$, $d = .56$) and were significantly greater than the geometric mean (600 ms; $t(7) = 7.95$, $p < .001$, $d = 2.80$).[6] Furthermore, normalizing the PSEs from each testing phase by dividing it by the duration of the long anchor value revealed the relative location of the subsecond PSEs to be significantly greater than the suprasecond PSEs, $t(5) = 5.5$, $p < .003$, $d = 2.25$.

In contrast, the relative precision in responding (as measured by the Weber fraction) appeared unaffected by the range of signal durations presented (Subsecond: $M = .244$; Suprasecond: $M = .206$; $t(5) = 1.03$, $p > .3$, $d = .49$).

Discussion

Our findings are the first to reveal intact rats are able to respond systematically to signals in the subsecond duration range. Despite responding at chance levels when applying an ordinal rule to durations in the subsecond range in our ordinal task (Experiment 1), rats in Experiment 2 revealed a competence in timing subsecond durations suggesting that an inability to represent short durations was not a factor in our first experiment.

Moreover, data reveal interesting asymmetries in the locations of the PSE for durations in the subsecond versus suprasecond range. Whereas suprasecond data mimic that of previous studies in humans and other animals revealing PSEs that approximate the geometric mean (Allan & Gibbon, 1991; Church & Deluty, 1977; Meck, 1983; Meck & Church, 1983; Penney, Gibbon, & Meck, 2008), subsecond data are distinctly different in that the PSEs were closer to the arithmetic mean of the two anchor values. Considering a substantial literature on nonhuman animal duration bisection tasks exists reporting PSEs falling at the geometric mean (e.g., Breukelaar & Dalrymple-Alford, 1998, 1999; Church & Deluty, 1977; Meck, 1983; Meck & Church, 1983; Meck, Church, & Gibbon, 1985; Pleil et al., 2011), this pattern of distinctly different PSE locations as a function of the absolute value of the durations

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[6] Note, these analyses hold when rats 4 and 8 (who did not contribute to the suprasecond testing data) were excluded from analyses. Subsecond data consistently did not differ from the arithmetic mean ($M = 725.3$; $t(5) = 1.17$, $p > .29$, $d = .48$) but did differ significantly from the geometric mean, $t(5) = 5.92$, $p < .002$, $d = 2.41$ of the anchor values.
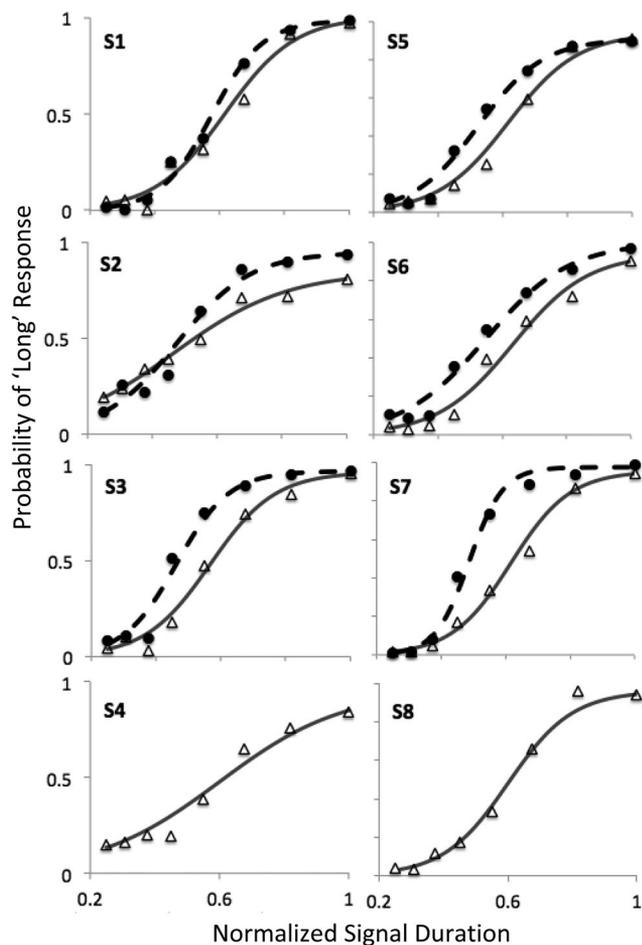
Figure 4. The probability of a "long" response for subsecond (open triangles) and suprasecond (filled circles) bisection test days as a function of the normalized duration of the signal (i.e., signal duration divided by the duration of the long anchor value; 1,200 [subsecond data] or 8 [suprasecond data]). Each plot represents data from a different subject (Subjects 1–8). The curves represent the best fitting sigmoid functions of the data (solid line for subsecond data, dashed line for suprasecond data).

tested may point to the involvement of two distinct cognitive processes underlying the representation of time in the subsecond and suprasecond ranges. Interestingly, a similar pattern has been reported with children and adults (Zélanti & Droit-Volet, 2011) and has been attributed to a difference in the ease of discrimination, such that easier discriminations lead to PSEs closer to the arithmetic mean (Wearden & Ferrara, 1996; Wearden, Rogers, & Thomas, 1997; Zélanti & Droit-Volet, 2011). According to this account, then our data suggest that subsecond discriminations should be easier (less cognitively taxing) for rodents than suprasecond ones.[7] If so, it is even more striking that rats in our first experiment failed to make systematic ordinal judgments across subsecond stimuli (despite their ease in discriminating these stimuli) yet succeeded in doing so for the more difficult suprasecond signals. Coupled with the finding that subsecond and suprasecond temporal discriminations yield distinctly different PSE locations (despite identical 4-fold changes in duration from the short to long

anchors; Wearden & Ferrara, 1996), results of Experiment 2 are suggestive of a two-system account of time representation, pointing to the employment of distinctly different cognitive processes for the representation of subsecond compared to suprasecond durations.

General Discussion

Results from our first experiment provide clear evidence that rats are capable of learning an ordinal rule, consistent with the findings of Santi et al. (2011). Rats performed significantly above chance in our task, revealing the rats appreciated the ordinal relationships inherent in continuous temporal quantities, applying the concepts of "longer than" or "shorter than" to durations ranging from less than 1 s up to 22 s. Importantly, correct responding required rats to attend to the durations of two distinct stimuli and perform an ordinal comparison between the Standard and the Comparison signal durations. Thus, our findings cannot be explained by attention to the duration of only one of the signals nor to the entire duration of both signals. Moreover, ordinal judgments were made *after* the presentation of relatively abstract signals (sounds and lights) that had no known hedonic value for the rats. This suggests that ordinal judgments were based upon relatively abstract representations of time located in working memory, indicative of a true abstract understanding of ordinality as described by Cordes, Williams, and Meck (2007).

In contrast to other studies, ordinal abilities were tested across a notably broader range of quantity (220-fold change in duration) spanning the subsecond and suprasecond ranges. This broad range of test durations opened the door to examine timing in the subsecond and suprasecond range within the same test session, providing a glimpse at a discontinuity in the mental time line. Notably, when the Standard and Comparison were shorter than 1 s, responding hovered around chance levels but as soon as the stimulus durations were longer than 1 s, responding was systematic and accurate. A number of reports suggest that timing in the subsecond and suprasecond ranges may be regulated by distinct neurological structures (e.g., Breukelaar & Dalrymple-Alford, 1999; Buhusi & Cordes, 2011; Buhusi & Meck, 2005; Ivry & Keele, 1989; Lewis & Miall, 2003a, 2003b). In line with these previous studies, our data are indicative of a similar disconnect between subsecond and suprasecond timing such that rats were able to generalize an ordinal rule to durations in the suprasecond range, but not for those less than 1 s. These findings are the first to demonstrate this subsecond/suprasecond distinction in a purely behavioral task with non-human animals.

It should be noted that initial ordinal training values were unevenly distributed across the suprasecond and subsecond ranges, with greater attention to the former. Training values were simply chosen so as to represent a wide range of values (500 ms to 12.5 s), with test values falling both within the training range (5.4 s) and outside of the range (100 ms and 22 s). If training exposure

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[7] Unfortunately, whether rats in our study perceived subsecond duration discriminations as easier than suprasecond ones is not something that can be gleaned from our data set. The nature of the bisection task does not allow for an examination of response accuracy since there is no objectively correct (or incorrect) response on intermediate probe values (Wearden & Lejeune, 2008)—responding was instead a function of the subjective similarity of values to the two anchor values.

accounted for our pattern of results, rats should also have responded at chance levels for our longest durations, in which they only received limited training exposure. But this was not the case. Our data clearly show a dissociation in response patterns that is independent of the values exposed to in training, suggesting that the specific training values used did little to influence our overall pattern of responses. If anything, we believe our findings that rats failed to generalize an ordinal response rule across the subsecond duration range are even more compelling because they did so *despite* (limited) prior experience with ordering in that range.

Importantly, data from our second experiment confirm that the chance levels of responding observed for subsecond duration ordinal comparisons was not due to an inability to discern the durations of the specific stimuli used nor due to a general inability in rats to represent durations in the subsecond range. When tested in a standard subsecond bisection task, rats were able to respond systematically with the probability of a "long" response increasing as a direct function of the duration of the stimulus presented. Although these findings are not surprising, these data are the first to characterize subsecond timing behavior of intact rodents, providing strong evidence to suggest that rodents are not different from humans in their timing abilities. Furthermore, these data strongly suggest that the pattern of results observed in our ordinal task is not due to a simple inability to discriminate subsecond durations but is instead indicative of the incompatibility of two distinct timing systems.

The idea of a disconnect in quantity representation is not unique—in fact, there is substantial evidence to suggest that humans and other animals represent *numbers* using two distinct cognitive systems (Agrillo et al., 2008; Cordes & Brannon, 2009; Feigenson, Carey, & Hauser, 2002; Hauser & Carey, 2003). Remarkably, human infants, monkeys, and even mosquitofish consistently fail to discriminate a small (<4) set from a large (>3) set despite discriminating set sizes within a given range (e.g., infants succeed in discriminating 2 from 3 but fail to discriminate 2 from 4) and also reveal marked impairments in discriminations of small sets from other small sets (e.g., 1 vs. 2) when continuous confounding variables (i.e., surface area) are controlled (Xu, 2003; see Anderson & Cordes, 2013, for review). Considering the prominent theories in the field of quantity representation posit time and number are represented via the same cognitive systems (Allman, Pelphrey, & Meck, 2012; Cantlon, Platt, & Brannon, 2009; Meck & Church, 1983; Meck et al., 1985; Walsh, 2003), it is not surprising that our data reveal remarkable parallels between representations of time and number, revealing a similar break in the mental time-line arising early in evolutionary history. Of note is that data from multiple studies suggest neural activation patterns for small values (small numbers AND short durations) selectively involve secondary brain areas distinct from those for large values (large numbers and long durations; e.g., Ansari, Lyons, van Eimeren, & Xu, 2007; Gooch et al., 2011; see Buhusi & Cordes, 2011, for review), suggestive of a unique and/or privileged status of small values in the brain. Furthermore, data from our task coupled with numerical discrimination data reveal dramatic discrimination failures for small temporal and numerical values. Thus, we suggest that this additional neural processing may in fact work to the detriment of the representation of small values. In the case of number, small values are treated as distinct from large ones, leading to dramatic discrimination failures in non-human animals

and preverbal infants. In the case of time, our data suggest rats (and likely other nonverbal species) may fail to recognize the ordinal relations inherent in these small values when intermixed with longer durations.

Open questions remain, however. Do rats fail to appreciate ordinal relationships for subsecond durations altogether, or is it only in the context of longer durations that they fail to generalize an ordinal rule to shorter durations? Future studies should follow-up with training the ordinal comparison task specifically within the subsecond range in order to determine if rats are capable of making ordinal judgments based on stimuli shorter than 1 s without the potential interference from the timing of suprasecond durations within the same session. In addition, research should investigate whether a similar behavioral dissociation is found in other species, including human infants or young children. It is conceivable that, as in the case of number, this break in the mental time line may be evident in behavioral data in a wide range of nonverbal subjects. Given remarkable similarities in behavioral timing data observed across species, it is likely that a similar dissociation may be found in preverbal human infants, provided a rich enough data set. Also, additional testing should explore whether the deficits observed in the subsecond range are also apparent for other arithmetic processes (i.e., Time-Left task: Cordes, King, & Gallistel, 2007; Gibbon & Church, 1981; see Gallistel, Gelman, & Cordes, 2006, for review). To date, studies of temporal arithmetic have focused solely upon arithmetic understanding in the suprasecond range in non-human species. It is of interest to determine whether a similar arithmetic competence exists in the subsecond range and/or whether infants are also capable of duration arithmetic. Lastly, this study opens the door for a number of neurobiological investigations of sub- and suprasecond timing in rats within the same sessions. Importantly, while previous studies involving ordinal discrimination training in rats and pigeons have involved extensive training in order to get the animals to learn the task, our blocked design significantly reduced the number of training sessions necessary to get animals to respond greater than chance. While Santi et al. (2011) reported rats requiring anywhere from 100 to over 250 sessions in order to learn the task, once our blocked training procedure began, all eight rats learned within 50 sessions. Thus, future ordinal investigations may benefit from the employment of our blocked training procedure.

In summary, our data provide strong evidence that rats are capable of understanding that one stimulus was "longer" or "shorter" than another. That is, not only do they know that 2 s *is different* from 8 s but also they know that 2 s *is shorter* than 8 s. These data also expand our knowledge of non-human ordinal appreciations by providing a systematic exploration of this ordinal understanding of durations across a wider range of values than previously studied. Consistent with neurobiological evidence, our results provide the first purely behavioral support for the existence of a discontinuity in the mental time line in non-human species, suggesting that rats easily used an ordinal rule to respond to stimulus durations in the suprasecond range, yet reveal marked impairments in determining the ordinality of durations in the subsecond range. Data from our second experiment further reveal interesting asymmetries in temporal discrimination functions for subsecond and suprasecond durations. Together, results provide some of the first behavioral evidence to support the existence of two operationally distinct timing systems.

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