Nonverbal representation of time and number in adults

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Abstract

A wealth of human and animal research supports common neural processing of numerical and temporal information. Here we test whether adult humans spontaneously encode number and time in a paradigm similar to those previously used to test the mode-control model in animals. Subjects were trained to classify visual stimuli that varied in both number and duration as few/short or many/long. Subsequently subjects were tested with novel stimuli that varied time and held number constant (eight flashes in 0.8–3.2 s) or varied number and held time constant (4–16 flashes in 1.6 s). Adult humans classified novel stimuli as many/long as monotonic functions of both number and duration, consistent with simultaneous, nonverbal, analog encoding. Numerical sensitivity, however, was finer than temporal sensitivity, suggesting differential salience of time and number. These results support the notion that adults simultaneously represent the number and duration of stimuli but suggest a possible asymmetry in their representations.
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1. Introduction

Time and number serve as ubiquitous units of measurement for nearly any event or object we encounter. While counting and timing may seem as disparate processes, it is not clear to what extent they share a common biological substrate. It has been suggested that nonverbal organisms keep track of number and time using a single mechanism (Meck & Church, 1983; Roberts, 1995; Roberts & Mitchell, 1994). Evidence for this claim comes from studies in which rats or pigeons were trained to discriminate auditory stimuli that varied in both number and duration (2 tones in 2 s vs. 8 tones in 8 s). Subsequent testing with novel stimuli that varied in just one dimension (2–8 tones in 4 s; 4 tones in 2–8 s) showed that animals spontaneously encoded information about both time and number and that the psychophysical function representing the probability that subjects categorized an intermediate value as long or many was virtually identical when time or number was varied. Further evidence implicating a single mechanism was an almost identical leftward shift in the psychophysical function for time and number when rats were administered methamphetamine before the counting/timing task (Meck & Church, 1983).

To account for this strong parallel between timing and counting, Meck and Church (1983) adapted an information-processing model of timing originally developed by Gibbon (Gibbon, Church, & Meck, 1984). In this model, the accumulation of pulses emitted from a pacemaker serves as a representation of the amount of elapsed time. By positing that the switch controlling the flow of pulses into an accumulator can act in one of three different modes, the *mode-control* model allows the accumulator to represent number as well as time (Meck & Church, 1983; Meck, Church, & Gibbon, 1985). The accumulated value provides a common currency for time and number representation and, using multiple switches and accumulators, an organism could quantify time and number simultaneously. More recently, this model has been revised to postulate that numerical and temporal integration may be carried out by a distributed neural circuit that includes cortical areas activated by both timing and counting tasks (Buhusi & Meck, 2005).

Conflicting evidence, however, suggests that a potential dissociation exists between the representations of time and number in animals. For example, rats trained to perform the same bisection of auditory sequences have been shown to preferentially discriminate sequences on the basis of duration rather than number (Breukelaar & Dalrymple-Alford, 1998). Comparable discrimination of both number and time subsequently became apparent when the rats were cued to attend to numerical information. Pigeons trained to count or time on cue showed interference when they were cued to switch from timing to counting, but not from counting to timing (Roberts, Coughlin, & Roberts, 2000). In our own preliminary studies, we found a monkey to be more sensitive to the duration of a sequence of light flashes than its number (Roitman, Andrews, Brannon, & Platt, 2003). With further training, in which the monkey was cued to attend to number, we found comparable sensitivity to both variables.

Data from human studies have also shown biased interactions between time and number processing. In human children, numerical information has been shown to interfere with judgment of duration, although duration did not affect numerical judgments (Droit-Volet, Clement, & Fayol, 2003). Similarly, the number of flashes of a visual sequence interfered with duration judgments in a Stroop task, but their duration did not affect numerical judgments (Dormal, Seron, & Pesenti, 2006). In a dual-task paradigm,

tracking, visual search, and arithmetic distracters all interfered with concurrent interval timing. But, of the three types of distracters, only arithmetic performance was disrupted by concurrent interval timing when compared with a single-task condition (Brown, 1997). Temporal intervals are reproduced as shorter when fewer cycles of periodic stimuli are presented (Macar, 1996). A possible explanation for these findings is that temporal and numerical processing are carried out by common neural resources that limit the processing of both simultaneously. Together, these studies suggest that encoding of numerical and temporal information may rely on common neural substrates, which may be differentially influenced by relative salience and/or task demands.

Although it is incontrovertible that adult humans are capable of linguistically mediated number representation, building evidence suggests that they also possess a nonverbal system of representing numbers that follow the same principles observed in non-human animals (Gordon, 2004; Moyer & Landauer, 1967; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004; Pica, Lemer, Izard, & Dehaene, 2004). For example, when adult humans are asked to produce n responses, or estimate n events rapidly without verbal counting (Cordes, Gelman, Gallistel, & Whalen, 2001; Whalen, Gelman, & Gallistel, 1999), their behavior is virtually indistinguishable from rats tested in the same general paradigm (Platt & Johnson, 1971). Similarly, when monkeys or college students compare the relative numerical magnitude of two visual arrays, their accuracy and reaction time is dependent on the ratio of the two values and performance is very similar between the two species (Cantlon & Brannon, 2006).

It has been suggested that this analog magnitude representation of number is accomplished by means of a spatial 'number line', possibly exploiting the organization of space encoded in parietal cortex (Hubbard, Piazza, Pinel, & Dehaene, 2005). Regions within posterior parietal cortex (PPC) encode spatial information used to guide eye and hand movements in both humans and monkeys (Rizzolatti, Luppino, & Matelli, 1998; Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002). The classic tetrad of symptoms found with Gerstmann syndrome (acalculia, finger agnosia, disorientation of right and left space, and agraphia), suggest a necessary role for parietal cortex in the representation of quantity as well as space (Gerstmann, 1940; Roeltgen, Sevush, & Heilman, 1983). Further evidence for spatial coding of number derives from the SNARC effect in which smaller (larger) numbers are responded to faster with the left (right) as if the mental 'number line' is mapped onto spatial representation from the right to left hemisphere (Dehaene, Bossini, & Giraux, 1993). This relationship between space and quantity has been shown to be amodal (Nuerk, Wood, & Willmes, 2005), and also maps from top to bottom (Ito & Hatta, 2004; Schwarz & Keus, 2004). Similarly, grip closing (opening) has been shown to be faster following small (large) numerical digit presentation (Andres, Davare, Pesenti, Olivier, & Seron, 2004).

A common foundation for these relationships may be a feature of neural processing in PPC. Parietal lesions are associated with numerical deficits in patients (Dehaene & Cohen, 1997; Molko et al., 2003), and processing of both symbolic and non-symbolic numerical stimuli by normal subjects activates PPC (Fias, Lammertyn, Reynvoet, Dupont, & Orban, 2003). The recovery of the BOLD signal to novel numerosities following habituation of neural responses to a standard value suggests tuning for quantity in the intraparietal sulcus (Piazza et al., 2004) similar to that observed in single neuron recordings in monkey (Nieder & Miller, 2004). Further implicating a role for parietal cortex in human numerical judgments is the finding that the bias of overestimating the difference between a centrally-

viewed number and one presented to the left is suppressed by repetitive transcranial magnetic stimulation of posterior parietal cortex (Oliveri et al., 2004).

A role for PPC has also been proposed for temporal processing. Nonhuman primate studies have shown that single neuron responses in posterior parietal cortex are modulated by judgments of short (<2 s) intervals (Leon & Shadlen, 2003) and anticipatory responses based on the hazard function of elapsed time (Janssen & Shadlen, 2005). And, just as interactions between space and number have been reported, a patient with neglect of left space has been shown to overestimate the duration of stimuli presented in neglected space (Basso, Nichelli, Frassinetti, & di Pellegrino, 1996). These interactions between number, space, and time have been integrated in a proposed 'theory of magnitude', in which these units of measurement share a common neural basis in the PPC as well as prefrontal cortex, basal ganglia, and cerebellum (Walsh, 2003). Buhusi and Meck (2005) likewise propose a more distributed network substrate for interval timing and counting that modifies the accumulator model to a more biologically plausible system that encompasses these same neural structures.

Thus, psychophysical and neurobiological studies collectively support the idea of functional overlap or interaction between neural circuits processing time and number. If a shared neural system indeed processes both time and number, one would predict comparable encoding of each variable in adult humans, even without any verbal instruction or under conditions of verbal distractions. To test this idea, we adapted the numerical and temporal bisection task used by Meck and Church (1983) to test whether adult humans, like rats, spontaneously track both the number and duration of a sequence of events using a single mechanism. Their experimental paradigm was modified to allow direct comparisons between humans and monkeys (Roitman et al., 2003), providing a foundation for physiological recordings in monkeys using the same task to measure how time and number may be encoded in the activity of single cortical neurons. In Experiment 1, adult humans were trained, without any explicit verbal instructions, to discriminate compound visual stimuli that varied in both time and number. They were then tested, without feedback, with randomized novel stimuli that varied in one dimension while holding the other constant. The specific properties of the visual sequences were selected to minimize the contribution of verbal counting. Our question was whether time, number, or both would control behavior.

2. Experiment 1

2.1. Method

2.1.1. Subjects

Twelve undergraduate volunteers from Duke University with normal or corrected-to-normal vision gave consent to participate in the study (6 male). The Duke University Health System Institutional Review Board approved all procedures.

2.1.2. Apparatus

Subjects sat facing a 15 in. LCD computer monitor (resolution 1024×768, refresh rate 75 Hz), with their heads held stationary in a chin rest at a viewing distance of 15 in. Subjects responded by pressing a touch-screen (*MagicTouch*) attached to the computer monitor and sampled at 125 Hz. Stimuli were presented and behavioral responses collected by a computer running custom software (ryklinsoftware.com).

2.1.3. Visual stimuli and bisection task

2.1.3.1. Training. Each experimental session began with a set of approximately 50 training trials. On each trial, one of the two *compound stimuli*, 4/short or 16/long (Fig. 1A), was randomly presented. Each trial began with the illumination of a central yellow fixation point (FP). Subjects were instructed to touch the FP to begin the trial and to continue looking at it throughout the trial. Following a 400 ms delay, two response targets appeared 10° below the fixation point, separated by 22°. Next the compound stimulus began, which was a yellow circle flashing either 4 or 16 times 10° above the FP. Each flash lasted 50 ms, with a 150 ms inter-stimulus interval (ISI); the sequences of 4 and 16 flashes thus lasted 0.8 and 3.2 s, respectively.

To equate the overall duration of the two types of training trials, a delay of 2.4 s was imposed between the onset of the response targets and the first flash of the 4/short sequence. This pre-stimulus delay discouraged subjects from using cues that might otherwise be confounded with the trial-to-trial structure, rather than attending to the stimulus
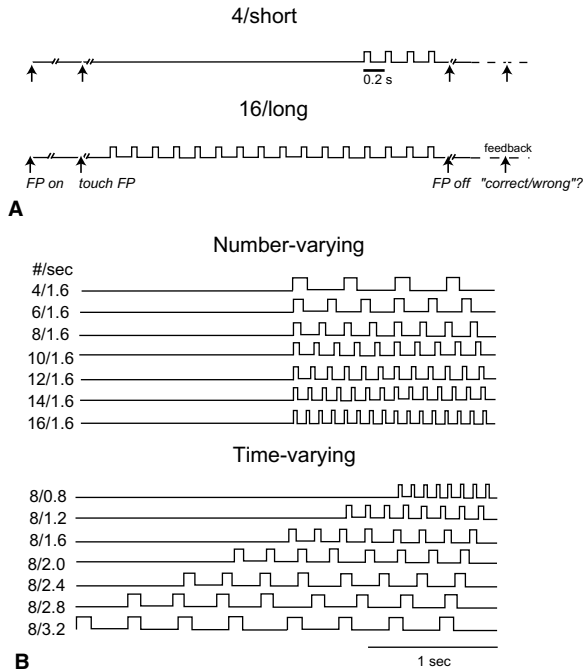

Fig. 1. Stimuli tested in numerical and temporal bisection task. (A) *Compound training trials.* Subjects were trained to discriminate stimuli that varied in both time and number, 4/short vs. 16/long. Each trial began with the illumination of a fixation point (FP). Subjects touched the FP and maintained gaze on it throughout the trial. Following a 400 ms delay after the FP was touched, two response targets appeared, and one of the compound stimulus types was presented, which subjects were instructed to attend. Immediately following the end of the final cycle, the FP was extinguished which cued subjects to touch a response target. Feedback ("correct''/"wrong") was given on compound trials. (B) *Novel test stimuli.* Trial sequence was the same as compound stimuli, except the stimulus was replaced with one that varied either time or number. In number-varying stimuli, the number of flashes ranged from 4 to 16, each presented in 1.6 s with a 1.6 s delay preceding cue onset. In time-varying stimuli, the number of flashes was held constant at 8, which were presented in 0.8–3.2 s with a delay preceding first flash onset that varied from 0 to 2.4 s.

sequence. First, as noted, the delay matched the overall duration of the two training trial types. This is important since subjects were required to fixate throughout the trial and overall fixation time would be a potent discriminable cue. In a preliminary study with macaques, we found that total fixation time was the sole basis for discrimination of stimuli in training trials, regardless of the temporal structure of the stimuli when no pre-stimulus delay was used (Roitman et al., 2003). Equating this interval encouraged subjects to attend to the events within the trial, rather than the interval between the on- and offset of fixation. During the test phase of the experiment, the delay provided a randomized foreperiod between response target and stimulus onsets (Green, Smith, & von Gierke, 1983). This randomization bolsters the saliency of the onset of the stimulus by reducing its predictability. Although this delay was only present on 4/short trials and thus could have provided an additional cue, it should be emphasized that subjects were instructed to attend to the sequence of flashes and base their choices on them.

Following the last flash, the FP was extinguished, cuing the subject to respond by touching either the red or green target. Subjects were only told that they would receive feedback about their choices, and should deduce which target corresponded to which stimulus. After touching a target, the word 'Correct' was displayed if subjects chose the green target following 4/short or the red target following 16/long. Incorrect choices were followed by the word 'Wrong' on the screen.

2.1.3.2. Testing. Subjects were tested with a numerical and temporal bisection task, in which they classified novel stimuli varying in either number or duration (Fig. 1B, Table 1). In 'number-varying' stimuli, duration was held constant at 1.6 s while the number of flashes ranged from 4 to 16. In 'time-varying' stimuli, eight flashes were presented over durations ranging from 0.8 to 3.2 s. The 13 novel stimulus types were each randomly interleaved among compound stimuli on approximately 4% of trials, and were unreinforced.

Table 1
Temporal properties of compound and novel stimuli

Stimulus	Cycle on (ms)	Cycle off (ms)	Total on (s)	Total dur (s)	Rate (Hz)
4 in 0.8 s	**50**	**150**	**0.2**	**0.8**	**5.0**
16 in 3.2	**50**	**150**	**0.8**	**3.2**	**5.0**
4 in 1.6	100	300	0.4	1.6	2.5
6 in 1.6	67	200	0.4	1.6	3.8
8 in 1.6	50	150	0.4	1.6	5.0
10 in 1.6	40	120	0.4	1.6	6.3
12 in 1.6	33	100	0.4	1.6	7.5
14 in 1.6	29	86	0.4	1.6	8.8
16 in 1.6	25	75	0.4	1.6	10.0
8 in 0.8	25	75	0.2	0.8	10.0
8 in 1.2	38	112	0.3	1.2	6.7
8 in 1.6	50	150	0.4	1.6	5.0
8 in 2.0	63	187	0.5	2.0	4.0
8 in 2.4	75	225	0.6	2.4	3.3
8 in 2.8	88	262	0.7	2.8	2.9
8 in 3.2	100	300	0.8	3.2	2.5

Cycle on and *off* times are the durations of stimulus flashes and inter-stimulus-intervals. *Total on* is the cumulative amount of time that the cue is displayed. *Total dur* is the duration from the onset of the first flash until the offset of the final flash. *Rate* is the frequency of flashes, in Hz.

Compound stimuli were reinforced on 40% of trials and were unreinforced on 8% of trials. Subjects performed approximately 275–300 trials in the testing phase in order to view each novel stimulus at least 10 times. Test trials were embedded infrequently (52%) with training trials to encourage subjects to respond in the same manner as during training.

Subjects were informed that about half of the trials would be identical to those they had just performed, although a small proportion would be unreinforced. For the remaining trials, they were told to use the same decision rules for new stimuli that they would see, and that they would not receive feedback because there were no correct or incorrect answers.

2.1.4. Analysis
2.1.4.1. Individual subjects. Subjects were considered sensitive to a varying stimulus dimension (time or number) if there was a statistically reliable difference (*t*-test, $p < 0.01$) in the proportion of many/long choices for the *extreme novel* values for each stimulus type, i.e. 4 vs. 16 flashes (in 1.6 s) for number-varying, and 0.8 vs. 3.2 s (for eight flashes) for time-varying. To fully characterize psychophysical performance more, each data set, number- or time-varying, was fit by a cumulative normal function with free parameters of mean and standard deviation. The bisection point (BP), or value judged as equally similar to the two extreme values, was determined by the mean of the fit. Sensitivity was estimated by first calculating the difference limen (DL), or half the distance between the values that supported 0.25 and 0.75 many/long choices. The DL was used to compute the Weber fraction (WF), i.e. the ratio of DL:BP, an index of sensitivity relative to the values tested that is useful for comparing sensitivity across stimulus dimensions of number and time. Because some subjects failed to discriminate with 100% accuracy, the extreme novel values for each stimulus type, lower and upper asymptotes were also included as free parameters in the fit.

2.1.4.2. Population analyses. To compare discrimination of time- and number-varying stimuli separately across subjects, two methods were used to calculate population BP and WF, as in Droit-Volet and Wearden (2001). First, data from all subjects sensitive to each dimension were combined, and a cumulative normal function was fit to the *group* data. The group bisection point (BP_g), and group Weber fraction (WF_g) were estimated from the fit in the same manner as described above for individual subjects. Because subjects included in the group analysis were sensitive to the varying dimension, lower and upper asymptotes were not included as free parameters in the fit. Second, the population bisection point and Weber fraction were calculated as the mean of the values from sensitive *individuals* (BP_i and WF_i). This was done to prevent underestimation of the WF as a consequence of combining data from equally sensitive subjects that differed in BP.

2.2. Results

2.2.1. Compound stimuli
Subjects learned to classify compound stimuli accurately by trial-and-error. Once the initial stage of training was completed, subjects selected the 'many/long' target on 0.02 ± 0.01 of 4/short trials and 0.97 ± 0.02 of 16/long trials ($t = -35.78$, df = 22, $p < 0.0001$). The proportion of many/long choices on compound trials for individual subjects is shown in Table 2. Subjects judged these trial types almost faultlessly throughout the test session while novel, unreinforced trials were interleaved, confirming that they attended to the task and applied a consistent decision rule.

Table 2
Individual performance on compound and novel stimuli

Sub.	Compound			Number-varying				Time-varying			
	4/Short	16/Long	p	BP	WF	Range	R^2	BP	WF	Range	R^2
1	0.00	1.00	<0.001	**8.61**	**0.07**	0.97	0.99	**2.79**	**0.01**	0.51	0.86
2	0.00	1.00	<0.001	**7.64**	**0.03**	0.98	0.99	–	–	–	–
3	0.00	0.83	<0.001	**8.48**	**0.08**	0.93	0.99	2.07	0.002	0.29	0.43
4	0.00	1.00	<0.001	**11.89**	**0.02**	0.79	0.99	**2.82**	**0.13**	0.93	0.87
5	0.11	1.00	<0.001	**6.48**	**0.13**	0.97	0.99	–	–	–	–
6	0.00	1.00	<0.001	**8.54**	**0.14**	0.94	0.97	**2.35**	**0.34**	1.00	0.80
7	0.00	1.00	<0.001	**5.73**	**0.05**	1.00	1.00	–	–	0.00	–
8	0.02	0.98	<0.001	**6.71**	**0.21**	0.97	0.97	**1.20**	**0.31**	0.98	0.96
9	0.05	0.98	<0.001	4.79	0.42	0.39	0.33	**2.34**	**0.36**	0.89	0.97
10	0.06	1.00	<0.001	**5.89**	**0.04**	0.90	1.00	1.18	0.03	0.23	0.88
11	0.00	0.96	<0.001	**8.93**	**0.28**	1.00	0.94	0.84	0.04	0.38	0.39
12	0.00	1.00	<0.001	**5.37**	**0.06**	1.00	1.00	–	–	–	–

The proportions of many/long choices for 4/short and 16/long compound stimuli are shown, as well as the significance of the difference between the proportions. For number- and time-varying stimuli, data for each subject were fit with a cumulative normal function with the parameters of mean, standard deviation, and upper and lower asymptotes. The Bisection Point (BP) is the mean of the function, and the value judged as equally similar to the two extreme values (4/16 or 0.8/3.2 s). The Weber Fraction (WF) was calculated as an estimate of sensitivity relative to the BP (see Experiment 1, Methods). Range is the difference between the upper and lower asymptotes of the fit, and r^2 is proportion of variance accounted for by the fit. BP and WF are shown in bold for subjects who successfully discriminated the two extreme values of the novel stimulus sets ($p < 0.01$), and had both a range > 0.4 and $r^2 > 0.4$. Empty cells signify an inability to fit the data with a cumulative normal function.

2.2.2. Bisection by individual subjects

During the bisection task, probe stimuli randomly varied either the number of flashes *or* the duration of the flashing stimulus and subjects were not informed which was relevant for responding. Fig. 2 shows the proportion of many/long choices for novel number- and time-varying stimuli for each subject. Subjects were considered to be sensitive to a stimulus attribute (number or time) if there was a statistically reliable difference ($p < 0.01$) between the proportions of many/long choices for the *extreme novel* values for each stimulus type, i.e. 4 vs. 16 flashes (in 1.6 s) or 0.8 vs. 3.2 s (for eight flashes). The BP and WF are shown in bold type in Table 2 for subjects that met this criterion, and these subjects are included in the population analyses that follow.

Four of the twelve subjects (1, 4, 6 and 8) were sensitive to both number and duration of novel stimuli. Seven of the remaining subjects were sensitive to only numerical variation of novel stimuli (2, 3, 5, 7, 10, 11 and 12). Several pieces of evidence suggest that these subjects did not use temporal information to discriminate novel stimuli. As shown in Fig. 2, the proportion of many/long choices increased with the number of flashes in novel stimuli. However, these subjects failed to show a statistically reliable difference ($p < 0.01$) between the proportions of many/long choices for the extreme values for time-varying stimuli, i.e. 0.8 vs. 3.2 s for eight flashes. In addition, the cumulative normal functions to their full sets of data were either characterized by a poor fit ($r^2 < 0.4$), had a limited range between lower and upper asymptote (<0.4), or could not be fit at all. Finally, one subject's behavior was controlled by time and not number (9). A complete report of BP, WF, range (upper-lower asymptote), and quality of fit (r^2) for each subject is presented in Table 2.
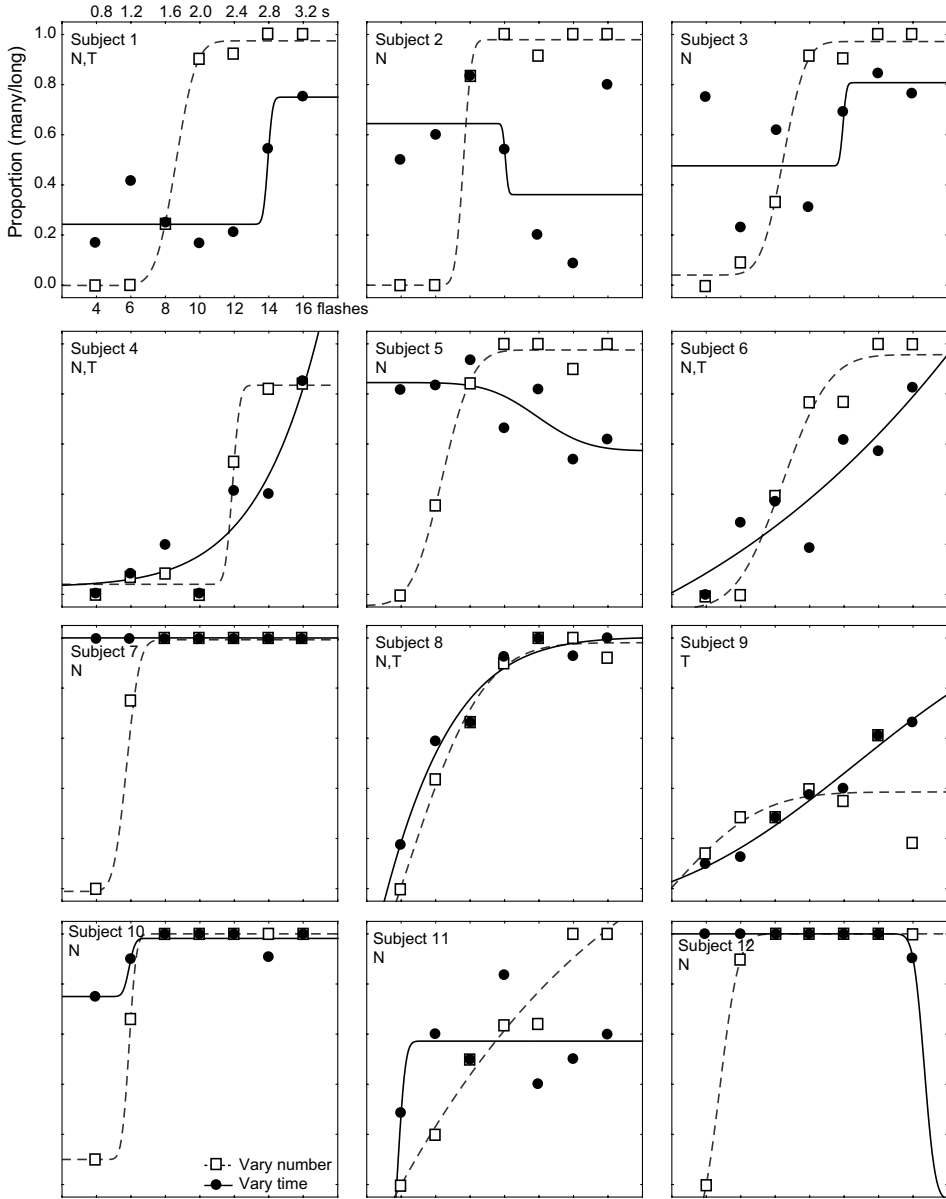
Fig. 2. Performance of individual subjects. The proportion of many/long choices is plotted as the number (open squares, dashed line) or duration (filled circles, solid line) of novel stimuli varied. The letters beneath the subject number indicated whether they were sensitive to number (*N*), time (*T*), or both.

2.2.3. Sensitivity to number

When the number of flashes varied but duration was constant, most subjects classified stimuli on the basis of number. Fig. 3 (open squares) shows the mean proportion of many/long choices as a function of the number of flashes presented in 1.6 s for the 11 of the 12 subjects sensitive to number. The bisection point estimated from the combined group data
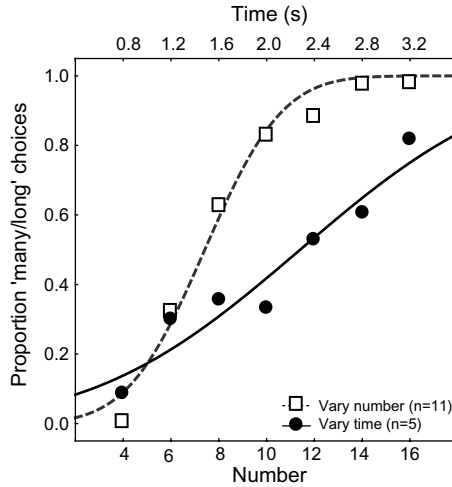
Fig. 3. Subjects judged novel stimuli according to number and duration of flashes. All novel trial types were interleaved with compound stimuli, and subjects were not told how to discriminate them. The proportion of many/long choices increased with greater number in the number-varying series (open squares, dashed line), and longer duration in the time-varying series (filled circles, solid line).

(BP$_g$) was 7.41, with a DL$_g$ of 1.72 and WF$_g$ of 0.23 ($r^2 = 0.980$). Calculating the average of bisection points from individual subjects (BP$_i$) yielded a similar estimate of 7.66. However, average sensitivity calculated from individual subjects was higher with a WF$_i$ of 0.10 (Table 3).

2.2.4. Sensitivity to duration

Some subjects also classified novel stimuli that varied in duration but were constant in number on the basis of time. The average probability (filled circles) of a many/long response as a function of the duration of eight flashes is shown in Fig. 3 for the five subjects of twelve sensitive to duration (see Fig. 2, Table 2). The BP$_g$ for temporal judgments was 2.28 s, with a DL$_g$ of 0.92 s, and WF$_g$ of 0.40 ($r^2 = 0.925$). For the five subjects sensitive to duration, the average BP$_i$ was 2.30 and WF$_i$ was 0.23. The differences between the two methods of estimating BP and WF are discussed more thoroughly below

Table 3
Comparison of BP and WF calculated from combined group (g) data or average of individual (i) data

Experiment		BP$_i$ (CV)	WF$_i$	BP$_g$	WF$_g$
1	Number	7.66 (0.25)	0.10	7.41	0.23
	Time (s)	2.30 (0.29)	0.23	2.28	0.40
2	Number	7.45 (0.11)	0.09	7.69	0.15
	Time (s)	1.74 (0.35)	0.08	1.63	0.44
3	Number	8.53 (0.24)	0.14	8.69	0.27
	Time (s)	2.72 (0.41)	0.22	2.50	0.45

For BP$_i$, the coefficient of variation (CV $= \sigma/\mu$) is listed for each average.

in Experiment 2. Although subjects classified time-varying stimuli on the basis of duration, they were clearly more sensitive to number than time in the bisection task.

2.2.5. Discussion

After being trained to discriminate stimuli in which the number of flashes in a sequence and sequence duration were confounded, some adults tracked both the number and duration of novel stimuli. Given that subjects were not instructed to time or count flashes nor were they given feedback about novel choices, it is not surprising that some subjects discriminated only one stimulus attribute. It is improbable to posit that any organism would track the number and duration of every sequence of events that they perceive. However, it is remarkable that even four out of 12 subjects tracked both time and number given that tracking either dimension alone could easily solve the training task. The data from unreinforced trials suggest that some adult humans implicitly encoded both the number of flashes and the sequence duration during training, consistent with the mode-control model.

Although the range of relatively large numbers (4–16) and short durations (0.8–3.2 s) tested minimized verbal counting by subjects, other aspects of the stimuli may account for differences in salience between time and number. Test trials varied in the rate at which the cue flashed, yet subjects did not appear to use this information to classify stimuli since flash rate increased with number but decreased with duration. Had they used rate, choice functions for time and number would have been inverted. While humans are able to judge single intervals on a time scale of tenths of seconds to seconds (Droit-Volet, 2002), the cyclical nature of the stimulus, coupled with randomized stimuli varying in number, may have contributed to the difficulty in judging the cue sequence duration. A final important caveat is that our modification of the Meck and Church procedure, which equates total fixation time, may have decreased salience for duration.

3. Experiment 2

A possible explanation for why subjects were more sensitive to number than time in Experiment 1 is that various temporal features of the trial structure may have reduced to the salience of time. To determine how well human subjects could discriminate the duration and number of events used in the sequences of Experiment 1, we replicated the experiment with explicit instructions to subjects to attend to either number or duration during separate blocks of number- or time-varying test stimuli.

3.1. Method

3.1.1. Subjects

An additional 9 subjects (5 male) were tested in the second experiment using identical apparatus and stimuli.

3.1.2. Bisection task

3.1.2.1. Training and testing. Training was identical to that of Experiment 1, except that subjects were verbally instructed to attend to the number of flashes or the duration of the sequence in separate blocks of trials. Following approximately 50 training trials, subjects performed a block of number- or time-varying trials, with order counterbalanced

across subjects. Subjects were instructed to continue using the same decision rule as in training. Each of the 7 novel trial types was unreinforced and presented randomly on 8% of trials. Reinforced and unreinforced compound stimuli were presented on 18% and 8% of trials, respectively. Each block typically lasted 140–150 trials. Upon completion of the first block, subjects were instructed to attend to the other stimulus dimension, given a brief set of practice trials, followed by the second block of novel stimuli.

3.2. Results

3.2.1. Compound stimuli
All subjects reliably classified compound stimuli accurately throughout the test sessions (Table 4). Following initial training, subjects chose the many/long target on 0.09 ± 0.05 of 4/short trials and 0.97 ± 0.01 of 16/long trials ($t = -72.7$, df = 16, $p < 0.0001$).

3.2.2. Bisection by individual subjects
In this experiment, probe stimuli that varied in either the number of flashes *or* the duration of the flashing stimulus were presented in counterbalanced blocks, and subjects were instructed as to which was relevant for responding. The performance of each subject is shown in Fig. 4. Seven of the nine subjects discriminated novel stimuli on the basis of the relevant dimension. The remaining two subjects (5, 9) successfully discriminated number, but failed on duration-varying trials. A complete report of subjects' BP, WF, and range estimated from cumulative normal fits to the subjects' data sets are presented in Table 4.

3.2.3. Sensitivity to number
When verbally instructed to attend to number, all subjects were sensitive to the number of flashes presented in 1.6 s (Table 4). Fig. 5 (open squares) shows the average proportion of many/long choices for all nine subjects tested. The data were well fit by a cumulative normal function (solid line, $r^2 = 0.986$), which estimated a BP_g of 7.69, DL_g of 1.13, and WF_g of 0.15. The average of individual data estimates a BP_i of 7.45 and WF_i of 0.09. The reduction in WF over Experiment 1 (see Table 3) represents an improvement in sensitivity to number.

Table 4
Performance of individual subjects given explicit instructions for blocked novel stimuli

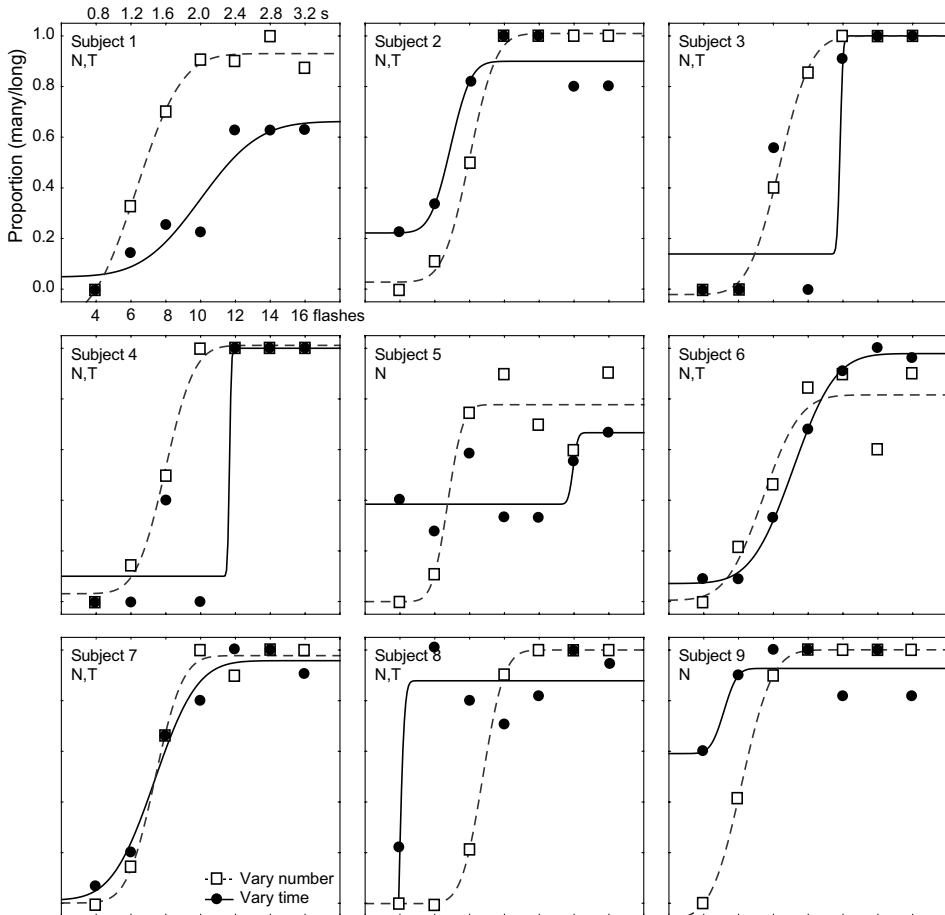| Sub.	Compound			Number-varying				Time-varying			
	4/Short	16/Long	p	BP	WF	Range	R^2	BP	WF	Range	R^2
1	0.00	1.00	<0.001	**6.73**	**0.17**	0.93	0.99	**2.00**	**0.18**	0.61	0.91
2	0.00	1.00	<0.001	**7.99**	**0.10**	0.97	0.99	**1.38**	**0.09**	0.68	0.93
3	0.00	0.83	<0.001	**8.08**	**0.03**	0.96	0.99	**2.15**	**0.01**	0.83	0.83
4	0.00	1.00	<0.001	**7.96**	**0.11**	0.97	0.99	**2.15**	**0.01**	0.90	0.92
5	0.11	1.00	<0.001	**6.74**	**0.07**	0.78	0.91	2.78	0.01	0.28	0.58
6	0.00	1.00	<0.001	**7.41**	**0.15**	0.81	0.90	**1.83**	**0.14**	0.91	0.99
7	0.02	0.98	<0.001	**7.37**	**0.11**	0.98	0.99	**1.47**	**0.18**	0.95	0.98
8	0.05	0.98	<0.001	**8.76**	**0.07**	1.00	0.9	**0.85**	**0.04**	0.78	0.83
9	0.00	0.96	<0.001	**6.02**	**0.01**	0.98	0.99	1.09	0.05	0.33	0.69

Fig. 4. Performance of individual subjects given instructions on blocked trials. The proportion of many/long choices is plotted as the number (open squares, dashed line) or duration (filled circles, solid line) of novel stimuli varied. Same conventions as in Fig. 2.

3.2.4. Sensitivity to duration

When verbally instructed to attend to time, seven of the nine subjects successfully discriminated eight flashes in 0.8 s from eight flashes in 3.2 s (Table 4). Because verbal instructions were provided, data from all subjects were included in the population average and are shown in Fig. 5. Here, average performance is plotted as a function of duration when time-varying stimuli were presented in a block under instructed conditions (filled circles). A cumulative normal fit to the data (dashed line, $r^2 = 0.92$) revealed a BP_g of 1.63 s, DL_g of 0.71 s, and WF_g of 0.44. Closer inspection of data from individual subjects (Table 4), however, shows that no single subject had a WF greater than 0.18. Calculated from the average of individual subjects, the BP_i was 7.45 and WF_i was 0.09. Temporal discrimination performance thus improved when stimulus duration was made more salient, in that it was successfully discriminated by a greater proportion of subjects and the WF for time was considerably lowered compared with Experiment 1.
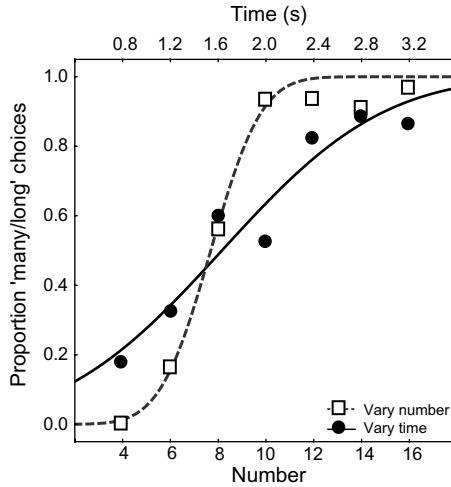
Fig. 5. Performance improved when subjects were instructed to attend to number or time of blocked trials. In each block of trials, number- or time-varying stimuli were presented separately and subjects were told which stimulus dimension to attend. Sensitivity to both number and time improved, compared with Experiment 1. Same conventions as Fig. 3.

3.2.5. Comparison of individual performance on numerical and temporal discrimination

To further assess subjects' relative sensitivity to number and time, we compared performance within subjects. The correlation between WF_{number} and WF_{time} is shown in Fig. 6. We found a positive relationship between sensitivity to number and time for individual subjects ($r = 0.71$, $p < 0.05$), and a linear regression with an intercept near zero (-0.010) and a slope near unity (0.973). Thus individual subjects tended to be equally sensitive to number and time when informed of the task demands.
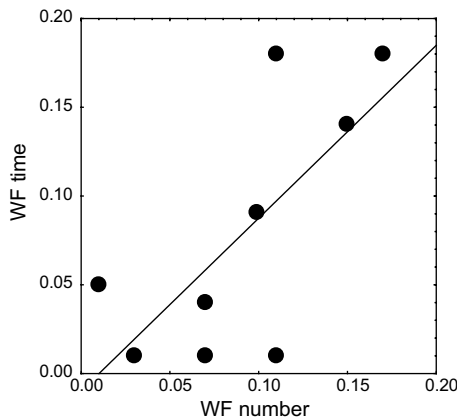

Fig. 6. Comparison of sensitivity to number and time for individual subjects. Each subjects WF for time is plotted as a function of their number WF. The data were fit with linear regression, with an intercept of -0.010 and slope of 0.973 ($r = 0.71$).

3.2.6. Discussion

Discrimination of both number and duration improved when subjects were instructed which stimulus attribute to judge in blocked trials. In this experiment, the pattern of results differed according to the statistical method used to calculate the population WF for number and time. Based on the combination of all subjects into a single *group* measure, subjects were again more sensitive to number ($WF_g = 0.15$) than time ($WF_g = 0.44$). However, estimates from the *average of individual* subjects revealed considerably greater sensitivity than to group estimates and showed no difference between sensitivity to number ($WF_i = 0.09$) and time ($WF_i = 0.08$). The discrepancies between the two methods of assessing the Weber Fraction arise from differences in variability in the BP of individual subjects in the two conditions. The BP indicates the criterion used by each subject to judge stimuli, which is represented by the location of the psychophysical curve, regardless of sensitivity to stimulus intensity, denoted by curve steepness. Variability in BP is listed in Table 3 as the coefficient of variation (CV) to enable comparisons across stimulus dimensions. In the case of number, a CV of 0.11 reflects that there was low variation in BP between subjects and consequently when subjects' data were combined, the resulting group estimate of sensitivity was close to the average of the individuals. In contrast, in the case of time, bisection points were more variable as reflected by a CV of 0.35. The combination of curves with similar steepness but different locations resulted in a group curve that was less steep (higher WF_g) than the individual curves that contributed to it (lower WF_i). As a consequence, sensitivity was underestimated by the group method in the time condition due to greater variability in the individual bisection points. It therefore appears that subjects discriminated novel numerical and temporal stimuli with comparable sensitivity in the blocked, instructed condition. A second consequence of describing BP and sensitivity from averaged group data is that choices appear to vary as a smooth, continuous function of number or time, when some individual's data may indeed be more step-like. This should serve in general as a caveat to the interpretation of group data, however, we have provided the individual data to enable comparisons between the subjects as individuals and averaged.

The range of durations (0.8–3.2 s) and numbers (4–16) tested were chosen to restrict subjects' ability to count flashes and track short intervals, i.e. by counting subintervals (Grondin, Ouellet, & Roussel, 2004). Event and inter-event intervals, which ranged for 25–300 ms, were selected to minimize the contribution of verbal counting. These stimuli depart from the typical ranges used in similar studies in animals and children (e.g. 2–8 in 2–8 s) (Droit-Volet et al., 2003; Droit-Volet & Wearden, 2001; Meck & Church, 1983; Roberts & Mitchell, 1994). These changes were adopted to decrease the duration that subjects (both human and monkey) would be required to fixate, and to reduce the likelihood of subvocal counting in humans. However, it is conceivable that subjects employed counting to enumerate and/or time visual stimuli.

4. Experiment 3

To further assess the possible role of verbal counting in Experiments 1 and 2, we sought to disrupt verbal counting by requiring subjects to perform a second verbal distracter task while making number and duration judgments. We used the methods of Experiment 1 (i.e., no instructions as to whether to attend to number or time), however the flashing yellow circle cue was replaced with flashes of 'A's and 'B's, in random order within a sequence.

Subjects first classified stimulus sequences as in the prior experiments, then reported the last letter of the sequence. This served to direct attention to the verbal task, with the aim of disrupting verbal counting.

4.1. Method

4.1.1. Subjects
Eleven naïve subjects (4 male) were tested in the third experiment. The testing apparatus was identical to that of the first experiment.

4.1.2. Visual stimuli and bisection task with verbal distracter
4.1.2.1. Training. Subjects initially learned to discriminate the two compound stimulus types, 4/short and 16/long, with two changes. First, the yellow circle cue was replaced with a yellow 'A' or 'B', the sequence of which was randomly selected on-line as the trial progressed. Second, after reporting whether the sequence was few/short or many/long (and given feedback), the question 'What letter flashed last?' was displayed on the screen followed by two choice targets, 'A' and 'B'. Subjects then touched the letter that corresponded to the last letter of the sequence. The subjects' instructions specified that the configuration of flashes that matched the response targets did not have to do with the letters themselves but other properties of the flashes, and that they should deduce the choice rule by trial-and-error. They were told to attend to the letters so that they could report the last letter that flashed after choosing the red or green target. After approximately 50–60 training trials, subjects proceeded to the testing phase.

4.1.2.2. Testing. In the testing phase, novel number- and time-varying stimuli were *both* randomly interleaved with compound stimuli, in the same manner as in Experiment 1. Subjects were given the same instructions about the test phase as Experiment 1, with the additional requirement of reporting the last letter seen on all trials.

4.2. Results

4.2.1. Compound stimuli
Replacing the flashing cue with a letter did not disrupt performance for classifying compound stimuli (Table 5). Subjects chose the many/long target for 0.04 ± 0.03 of 4/short trials and 0.95 ± 0.03 of 16/long trials ($t = -21.79$, df = 20, $p < 0.0001$).

4.2.2. Sensitivity to number
Performance in the third experiment was generally comparable to that in Experiment 1, in which all number- and time-varying stimuli were also randomly interleaved without specific instructions. Ten of the eleven subjects reliably discriminated 4 from 16 flashes presented in 1.6 s, and were able to classify novel stimuli according to number (Table 5). The proportion of many/long choices for each of the number-varying stimuli for these subjects is plotted in Fig. 7 (open squares). The fit to the bisection data (dashed line, $r^2 = 0.971$) showed the BP_g for number was 8.69, with a DL_g of 2.32 and WF_g of 0.27. Averages of individual data estimated a BP_i of 8.53 and WF_i of 0.14. These values suggest similar sensitivity to number in this testing condition as in the first experiment (Table 3).

Table 5
Performance of individual subjects classifying compound, number- and time-varying stimuli in the verbal distracter task

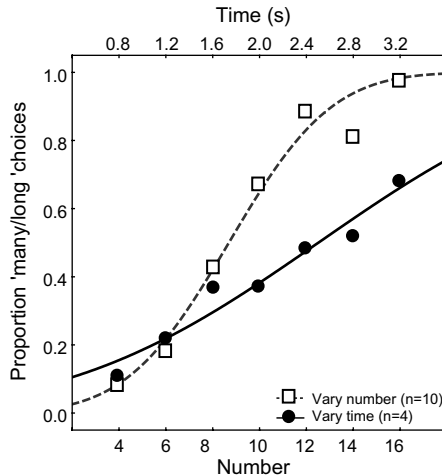| Sub.	Compound			Number-varying				Time-varying			
	4/Short	16/Long	p	BP	WF	Range	R^2	BP	WF	Range	R^2
1	0.04	0.90	<0.001	**9.23**	**0.13**	0.84	0.97	**3.40**	**0.39**	0.77	0.75
2	0.00	1.00	<0.001	**5.50**	**0.43**	0.97	0.97	0.72	0.15	0.77	0.33
3	0.02	0.98	<0.001	**6.66**	**0.39**	0.86	0.86	–	–	–	–
4	0.00	1.00	<0.001	**10.55**	**0.09**	0.82	0.92	–	–	–	–
5	0.00	1.00	<0.001	**9.11**	**0.30**	0.95	0.95	**3.91**	**0.92**	1.00	0.47
6	0.00	1.00	<0.001	**7.65**	**0.43**	1.00	0.96	–	–	–	–
7	0.00	1.00	<0.001	**12.89**	**0.31**	1.00	0.88	–	–	–	–
8	0.00	0.96	<0.001	**8.02**	**0.52**	0.88	0.86	**1.52**	**0.05**	0.64	0.97
9	0.35	0.72	<0.05	**8.01**	**0.05**	0.61	0.93	–	–	–	–
10	0.07	0.86	<0.001	–	–	–	–	**2.04**	**0.44**	0.99	0.95
11	0.00	1.00	<0.001	**7.67**	**0.07**	0.98	0.99	–	–	–	–

Fig. 7. Subjects discriminate number and time in the presence of a verbal distracter. The flashing cue (circle) of previous experiments was replaced with a series of 'A's and 'B's and subjects were asked to identify the last letter after classifying the series as few/short or many/long. All novel stimulus types were interleaved and no instruction was given, as in Experiment 1. Sensitivity to number and duration in the verbal distracter task was comparable to Experiment 1. Same conventions as in Fig. 3.

4.2.3. Sensitivity to duration

Temporal processing was also similar to that of Experiment 1. Four of eleven subjects distinguished stimuli based on duration (bold type, Table 5). Average proportions of many/long choices by these four subjects are shown in Fig. 7 (filled circles). The cumulative normal fit of the combined bisection data (solid line, $r^2 = 0.951$) estimated a BP_g of 2.50, DL_g of 1.13 s, and WF_g of 0.45. The average of individual subjects was BP_i of 2.72 and WF_i of 0.22. This level of sensitivity is roughly comparable to that found in Experiment 1.

4.2.4. Verbal distracter task

In the verbal distracter, subjects' ability to identify the last letter flashed was related to the number of flashed letters. On compound stimuli, subjects identified the final letter from the 4/short stimulus more accurately than the 16/long, despite equivalent cycle-on and -off times (0.90 ± 0.02 vs. 0.57 ± 0.02 correct choices; $t = 10.70$, df $= 20$, $p < 0.0001$). In number-varying test trials, the proportion of correct choices varied from near perfect for 4 flashes (0.92 ± 0.03) to chance following 16 flashes (0.51 ± 0.05). Overall performance varied with the number of letters in the series (linear regression, $r^2 = 0.35$, $p < 0.0001$). The intercept of the fit was 1.04 (CI $= 0.93$ to 1.15) with a slope of -0.034 (CI $= -0.044$ to -0.023). For time-varying stimuli, accuracy remained above chance, but did not systematically vary. On average, subjects identified the last letter correctly on 0.75 ± 0.02 trials, which did not differ across stimulus durations (ANOVA, $F = 0.62$, df $= 6$, $p = 0.71$).

4.2.5. Discussion

Overall the presence of a verbal distracter did not alter subjects' performance on the numerical and temporal discrimination task when compared with Experiment 1. However, performance on the letter identification in the verbal distracter task suggests that subjects divided their attention between sequence classification and letter identification throughout stimulus presentation. The inverse relationship between accuracy and number of flashes on letter identification revealed it to be a difficult task, and thus a successful distracter. Further, asking subjects to identify the *final* letter in the sequence may have maximized potential interference with temporal processing (Fortin & Masse, 2000).

The fact that subjects were able to discriminate number and time even while performing a difficult verbal distracter task suggests that they relied on a nonverbal representation of number and time. Anecdotally, subjects reported that viewing the flashing letters completely prevented verbal counting. They described that 'reading' the rapid series of letters, e.g. 'A A B A B B B A' seemed obligatory and did not permit simultaneous rapid counting, e.g. '1 2 3 4 5 6 7 8'. Yet they were able to discriminate the number of letter flashes and their duration as well as they had done in Experiment 1. The random ordering with the letter sequence may have contributed to the sense of it not being countable. Further experiments are needed to quantify the extent to which this and other distracter tasks disrupt verbal processing.

5. General discussion

Adult humans judged novel stimuli in a numerical and temporal bisection task according to the dimension that varied, suggesting that they implicitly encode information about both time and number. As did animals in previous studies, humans learned by trial-and-error to discriminate stimuli confounding number with time (Meck & Church, 1983; Roberts & Mitchell, 1994). When there were no instructions about which stimulus attribute was pertinent for their decisions (Experiments 1 and 3), some human subjects nonetheless categorized stimuli varying in either number or time according to the relevant dimension. The probability of classifying a stimulus as many/long increased with increasing number or stimulus duration. This suggests that a subset of subjects spontaneously encoded information about the number and duration of compound training stimuli and based choices on an analog representation of the relevant dimension. Although some subjects appeared to encode both time and number when the two cues were redundant, even these subjects

showed greater sensitivity to number than duration. This was evident by the smaller Weber fraction for number compared to time in Experiments 1 and 3.

A possibility remained that subjects were more sensitive to number because they relied on verbal counting and did not do so for discrimination of duration. To test this hypothesis, Experiment 3 incorporated a verbal distracter task in an attempt to disrupt verbal counting. Under these conditions, ten of the eleven subjects still discriminated number. For three of these subjects and one additional subject, the proportion of many/long choices was also related to sequence duration. This proportion is comparable to Experiment 1, in which four of the twelve subjects discriminated both time and number. For both number and time, sensitivity was not strongly affected by the verbal task, suggesting that performance did not depend on verbal counting. This conclusion would be strengthened by future replications of our task with additional verbal distracter methods.

Previous studies with animal subjects have also found asymmetries between time and number representation. Rats trained in the same time and number bisection task used by Meck and Church (1983) were found to preferentially classify novel stimuli varying in either time or number according to duration (Breukelaar & Dalrymple-Alford, 1998). However, when rats were cued to attend to numerical information their sensitivity to number increased. In another study, pigeons cued to attend to number spontaneously tracked duration, although those cued to discriminate duration did not also track number (Roberts et al., 2000). In contrast, in humans (adults and children), numerical information interfered with subjects' ability to discriminate duration, but time information did not interfere with number discrimination, suggesting that number processing is more automatic (Dormal et al., 2006; Droit-Volet et al., 2003).

In our study, performance was generally poorer on temporal than numerical discrimination. In Experiments 1 and 3, fewer subjects were sensitive to time than number, and sensitivity to number was greater (i.e. lower WF). But when given explicit instructions and blocked trials, most subjects successfully discriminated stimuli according to duration, and did so with sensitivity comparable to numerical discrimination. In general, the differences in sensitivity to numerical and temporal information suggest that number processing may be more automatic than time processing. Unlike animal studies in which subjects received extensive training with compound stimuli, our subjects were not expert psychophysical observers. Despite this, some subjects spontaneously extracted information about both stimulus attributes. It is possible that time discrimination of the stimuli used here was more difficult and would have improved with additional training.

Performance on temporal judgments may be particularly vulnerable to the difficultly of task demands. Directing attention to other task demands and stimulus properties interferes with accurate processing of temporal information (Brown & West, 1990; Brown & Boltz, 2002). Shifting attention to the discrimination of a nontemporal aspect of the stimulus results in a shorter estimate of its duration, presumably due to decreased attention to elapsed time (Casini & Macar, 1997). In particular, events occurring later in an interval to be timed produce shorter estimates of duration, presumably due to shifts in attention (Macar, 2002). Despite the disruption in timing, small amounts of practice improve performance, suggesting a benefit of increasing attentional resources (Brown & Bennett, 2002), as we found in Experiment 2.

When number- and time-varying stimuli were presented in a blocked design rather than randomized and accompanied by verbal instructions to attend to one dimension, subjects' showed greater sensitivity to time. This demonstrates that adults could easily discriminate

the ranges of stimuli used in this experimental paradigm. Moreover, greater sensitivity to both time and number may reflect the reduced attentional load provided by instructions and blocked trials. As consistent performance by individual subjects has been shown for temporal discriminations (Brown, 1998), we also found comparable sensitivity by individuals to number and time, reinforcing the notion of shared neural representations of these dimensions.

An essential tenet of the mode control-model is that once a stimulus is represented as an accumulated magnitude it should be functionally equivalent regardless of whether the original stimulus was discrete or continuous. In addition, number and time are hypothesized to be tracked automatically and simultaneously. The fact that number exerted more stimulus control than time in all three experiments suggests an asymmetry that is problematic for the mode-control model. Even if organisms have multiple accumulators operating on each stimulus and have the capacity to count and time a given stimulus, salience may effect whether number or time is tracked and how the outputs are combined and/or read out into a decision.

The value that is subjectively midway between the two extreme anchor values can be informative as to the psychological scaling of the subjective number line and the comparison rule an organism uses when comparing a sample to the two anchor values. A BP at the arithmetic mean implies a linear scaling of time and number, while a BP at the geometric mean suggests that the psychological scale is logarithmically spaced or linearly spaced but with variability that increases proportionally with magnitude. Studies in animals and humans suggest that the internal subjective number line is either logarithmic, or, equivalently, linear with scalar variability (Brannon & Terrace, 2000; Brannon, Wusthoff, Gallistel, & Gibbon, 2001; Dehaene, 2001; Gibbon & Church, 1981; Nieder & Miller, 2003; Platt & Johnson, 1971). Results from the numerical and temporal bisection task used by Meck and Church (1983) suggested that rats bisected compound stimuli at 4 tones/4 s, the geometric mean of 2 and 8, further supporting a nonlinear scale. Using a similar bisection task, human children were found to bisect the anchor values of 2 and 8 closer to the arithmetic mean (5) whether they were counting or producing non-counting speech, suggesting a linear representation of number (Droit-Volet et al., 2003). Our results are not perfectly consistent with either interpretation. In all three experiments, subjects bisected the compound stimuli closer to the geometric mean for number (8). Likewise, in Experiment 2, when task demands were explicit and attention was directed appropriately, subjects also bisected time-varying stimuli closer to the geometric mean (1.6 s). Without explicit instructions (Experiments 1 and 3), sensitivity for duration was reduced and BP's were more variable and closer to the arithmetic mean. Our results indicate that testing conditions, including stimulus salience and allocation of attention, influence how novel stimuli are judged in bisection tasks. We are cautioned from strictly interpreting the bisection point as the duration perceived as equally similar to the anchor durations because such stimulus attributes as duration range, ratio of the anchor stimuli, and spacing of probe stimuli between them do bias subjects' judgments (Allan, 2002; Wearden & Ferrara, 1995, 1996).

In conclusion, these results provide further support for the hypothesis that adult humans share with animals a nonverbal mechanism for representing number as continuous quantities (Brannon & Terrace, 2002; Cordes et al., 2001; Whalen et al., 1999) because even under conditions of a verbal distracter task, adults categorized novel stimuli as many/long largely as a smooth function of number. Future bisection studies testing the

superimposition of different ranges of values would bolster the idea that discrimination is based on analog coding of numerical and temporal magnitude. Our finding that a subset of our subjects spontaneously tracked both time and number suggests that subjects may automatically encode both the temporal and numerical attributes of stimuli in some circumstances, as predicted by the mode-control model. However, it is important to note that the results do not rule out the possibility that adults track time and number with distinct mechanisms. Finally, the asymmetry found between the sensitivity to time and number adds to previous challenges of the mode-control model and confirms previous arguments that attentional load and salience are important factors that determine how well number or time is tracked (e.g., Droit-Volet et al., 2003). In sum, further studies are needed to pinpoint whether time and number are represented with a single interchangeable currency as suggested by the mode-control model and how the relative salience of stimulus attributes affects the processing of time and number.

Acknowledgement

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