

Novel Inversions in Auditory Sequences Provide Evidence for Spontaneous Subtraction of Time and Number

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Abstract

Animals, including fish, birds, rodents, non-human primates, and pre-verbal infants are able to discriminate the duration and number of events without the use of language. In this paper, we present the results of six experiments exploring the capability of adult rats to count 2–6 sequentially presented white-noise stimuli. The investigation focuses on the animal's ability to exhibit spontaneous subtraction following the presentation of novel stimulus inversions in the auditory signals being counted. Results suggest that a subtraction operation between two opposite sensory representations may be a general processing strategy used for the comparison of stimulus magnitudes. These findings are discussed within the context of a mode-control model of timing and counting that relies on an analog temporal-integration process for the addition and subtraction of sequential events.

Keywords

Duration discrimination, number discrimination, temporal integration, mathematical ability, perceptual grouping

1. Introduction

How non-human animals and pre-verbal infants are able to represent the numerical attributes of a simultaneous array of objects or a series of sequential events is of considerable interest due to the implications for the types of mathematical concepts that can be mastered without the use of language. The representation of

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numerical quantities, such as discrimination of sets of objects containing a different number of items, has been demonstrated in a wide variety of animals including humans, monkeys, dolphins, lizards, birds, fish and rodents (e.g., Agrillo et al., 2008, 2012; Brannon & Terrace, 1998; Cantlon & Brannon, 2006, 2007; Dacke & Srinivasan, 2008; Jordan et al., 2008; Kilian et al., 2003; Pepperberg, 2006; Rugani et al., 2009; Uller et al., 2003; Xia et al., 2001). Even amongst humans research suggests pre-verbal human infants possess a representation of numerical attributes, as incorrect additions and subtractions elicit substantially prolonged looking times (Barth et al., 2006, 2008; Gilmore et al., 2007, 2010; Slaughter et al., 2006). Furthermore members of the Mundurucú Amazonian tribe, with a very small lexicon of number words, have been found to not only possess a sense of number, but even in the absence of formal mathematical training show similar performance on approximate number representation tasks as educated, Western adults (McCrink et al., 2012; Pica et al., 2004). This remarkable correspondence across species in the absence of language skills to discriminate among stimuli based upon number when other stimulus dimensions are controlled suggests the existence of innate shared computational mechanisms capable of recognizing and manipulating time and numerosity in a flexible manner (e.g., Church & Meck, 1984; Cordes & Meck, in press; Cordes et al., 2007; Fernandes & Church, 1982; Gibbon & Church, 1990; Gibbon et al., 1984; Hauser & Carey, 2003; Hauser et al., 1996, 2000, 2002; MacDonald et al., 2014; Mechner & Guevrekian, 1962; Meck, 1983, 1985, 1997; Meck et al., 2013).

These ontogenetically and phylogenetically shared numerical abilities are proposed to rest on the foundations of two core systems: one for the precise representation of small numbers of individual objects and a second representing large, approximate numerical magnitudes (e.g., Barth et al., 2003; Brannon & Roitman, 2003; Buhusi & Cordes, 2011; Feigenson et al., 2002a, b, 2004; Uller et al., 1999). The specific form of these distinct, but perhaps complementary, ‘counting’ devices has ranged from proposals for an object-file system that is able to accurately represent small quantities (e.g., up to four items) to an analog magnitude-estimation system that provides for approximate large number quantification based on the temporal integration of stimulus events (e.g., Brannon & Roitman, 2003; Flombaum et al., 2005; Gallistel & Gelman, 2000; Gelman & Gallistel, 1978; Gelman et al., 1986; Gilaie-Dotan et al., 2011; Meck, 1997, 2003; Meck & Church, 1983; Sulkowski & Hauser, 2001; Wynn, 1998).

1.1. Representation of Time and Number

When tested with sequences of temporally distinct events such as sounds, a number of species have shown the ability to classify sound sequences as being closer to ‘few’/‘short’ (e.g., two sounds/2 s) or ‘many’/‘long’ (e.g., six sounds/6 s) anchor points. These numerical and temporal discriminations are typically confounded by the nature of the compound stimulus presentation, but can be separated by holding one dimension constant and varying the other to reveal that classifica-

tion can be driven by either time or number (e.g., Brannon et al., 2001; Breukelaar & Dalrymple-Alford, 1998, 1999; Droit-Volet et al., 2003; Meck & Church, 1983; Roberts, 1995; Roberts & Mitchell, 1994; Roitman et al., 2005; Santi & Hope, 2001; Santi et al., 2001). Although some experiments find greater control by time or number, perhaps as a function of unspecified experimental parameters, the general finding is that a form of equivalence exists between these dimensions as a function of the ratio of the comparison stimuli. A quantitative similarity between duration and number has also been demonstrated for (1) the magnitude of cross-modal transfer between auditory and visual stimuli, (2) the enhancement in the rate of temporal integration as a function of stimulant drug administration, (3) the equivalence between the analog representation of the number of items and a specific duration, i.e., one count is equal to a fixed amount of time and these counts/times can be accumulated in order to determine the final value representing the set items (see Allman et al., 2012; Balci & Gallistel, 2005; Buhusi & Meck, 2005; Lustig, 2011; Meck, 1997; Meck & Church, 1983; Meck et al., 1985; Merchant et al., 2013). Nevertheless, there are some divergences in the processing of duration and numerosity when it comes to conflict paradigms (e.g., Agrillo et al., 2010), neurological dysfunction (e.g., Dormal et al., 2012a), and in the effects of emotional arousal as conveyed by neutral, happy, and angry faces (e.g., Droit-Volet & Meck, 2007; Young & Cordes, 2013).

1.2. Evidence for Transfer of Numerical Ordering and Spontaneous Subtraction

In order to extend the analysis of the magnitude-estimation mechanisms initially identified in rats and pigeons, it has proven useful to explore the types of numerical cognition displayed by non-human primates who may possess a greater degree of flexibility in their behavioral repertoire that can be related to more extensive cortical development (e.g., Brannon & Terrace, 2002; Carey, 1998; Dehaene et al., 2004; Nieder, 2005; Nieder & Miller, 2003, 2004a, b; Nieder et al., 2002; Pessoa & Desimone, 2003; Roitman et al., 2012). An excellent example of such an evolutionary comparison is provided by Brannon and Terrace (1998, 2000) who have shown that rhesus monkeys can be trained using appropriate reinforcement contingencies to discriminate among the numbers one through four and this training can then be transferred, without an explicit reinforcement rule, to discrimination among the numbers one through nine. These behavioral data demonstrating the numerical ordering of visual objects by monkeys have been used to provide support for the phylogenetic continuity of an analog magnitude-estimation mechanism because the number of items discriminated exceeded the limits of the proposed object-file mechanism (i.e., greater than four) and the observation that the accuracy of performance was dependent upon distance effects, i.e., greater accuracy with increasing differences between number pairs (see Feigenson et al., 2004; Uller et al., 1999).

Complementing the ability of animals to add successively presented stimuli and to transfer these discriminations to larger numbers, there is also compelling

evidence for spontaneous subtraction in rhesus monkeys that parallels the earlier work with pre-verbal human infants reported by Wynn (1992). In the basic design, one quantity of objects (e.g., plums) was presented on one stage and a second quantity of objects presented on a second stage. Both stages were then occluded and one or no objects were observed being removed from each stage. Having watched these events, monkeys were then allowed to approach one stage and eat the food objects behind the curtain. Results showed that monkeys correctly compute the outcome of subtraction from initial groups of three or fewer objects on each stage, even when the identity of the objects is different. This preference was also maintained when monkeys had to distinguish food from non-food subtractions, and when food was subtracted from both initial quantities (Sulkowski & Hauser, 2001).

1.3. Relationships to Mathematical Reasoning

Counting and arithmetic principles have been considered mutually constraining because counting produces cardinal values that can be added, subtracted, or ordered in accordance with the types of mathematical transformations required for arithmetic reasoning (Gelman, 2000; Zur & Gelman, 2004). Research has shown that mental computation is a valid method that contributes to mathematical thinking as a whole (e.g., Joram et al., 1998; Sowder, 1990). Indeed Halberda and colleagues (2008) demonstrated that standardised measures of mathematical achievement performed in children correlated strongly ($\sim 30\%$) with measures of number representaton abilities. More remarkably, aproximatley 14% of the variance in performance could still be captured when the two measures were taken nine years apart, suggesting a profound and long-lasting link between number abilities and real-world mathematical performance. Such mental computation is also a process for which young children have exhibited a variety of proficient spontaneous strategies for addition and subtraction operations that are contrary to instruction (Cooper et al., 1996). Although relatively little research has been conducted on the ability of non-human animals to perform subtraction operations (e.g., Brannon et al., 2001; Sulkowski & Hauser, 2001) there is a substantially larger literature on the types of mental calculation strategies used by children to learn addition and subtraction of whole numbers (e.g., Cohen & Marks, 2002; Fuson, 1984, 1986a, b, 1992; Fuson & Willis, 1988; Seyler et al., 2003; Vilette, 2002; Wynn, 1992). Moreover, these findings suggest that training children to use an approximate number system improves math proficiency by enabling the mapping of number words onto representations of these analog magnitudes (e.g., Park & Brannon, 2013; Pinas et al., in press).

Recent electrophysiological evidence from rats and monkeys suggests the existence of general purpose decision mechanisms that are able to contrast information from the accumulation of sensory inputs that represent both additions and subtractions, providing evidence that a subtraction operation can be performed spontaneously (e.g., de Lafuente & Romo, 2003; Ditterich et al., 2003; Heinz &

Formby, 1999; Matell & Meck, 2004; Mazurek et al., 2003; Thaut, 2003). Consequently, our goal in this study was to identify conditions in which rats have the opportunity to apply their experience of counting predictable sound sequences to novel situations where the spontaneous subtraction of events would be possible. The observation of spontaneous subtraction in the absence of explicit training addresses the issue of early competence and allows for the investigation of its properties, i.e., can subtraction result in the representation of a negative value?

2. General Methods

2.1. Subjects

Experiments were conducted with eight male Sprague-Dawley rats about 4 months of age and weighing 200–300 g (Charles-River Laboratories, Kingston, NY) at the beginning of the experiment. Rats were bred and raised as described by Meck and Williams (1997) and were housed in pairs in a 12:12 light:dark cycle with lights on from 7:00 AM to 7:00 PM. Rats were given continuous access to water and maintained at 85% free-feeding weight by a daily ration of Purina rat chow given shortly after the daily session. All procedures were conducted in accordance with the policies of the Institutional Animal Care and Use Committee.

2.2. Apparatus

The rats worked in eight standard-sized lever boxes with roof and side walls made of transparent acrylic and the front and back walls of aluminum. The floor was constructed of 16 parallel stainless-steel bars. Each lever box contained two retractable stainless-steel levers, one on each side of the food cup. A pellet dispenser delivered 45 mg precision food pellets. Each lever box contained a 10-W houselight and a programmable sound generator could deliver white noise of varying intensities (e.g., 50 and 90 dB) above background level through a speaker mounted inside each box. Lever boxes were housed inside insulated chambers designed to minimize outside light or sound. A time-shared IBM-PC compatible computer controlled the experimental equipment and recorded the data.

2.3. General Experimental Procedure

2.3.1. Pretraining

Each rat received four sessions of combined magazine and lever training. During these sessions a food pellet was delivered once each minute for 60 min (magazine training), and in addition, each lever press produced food (lever training). The left lever was inserted and 10 responses were reinforced; then the left lever was retracted and the right lever inserted; 10 right lever responses were reinforced; then the right lever was retracted and the left lever was again inserted. This alternation between levers continued until the rat had pressed each lever 60 times or 60 min had passed, whichever came first. The houselight illuminated the chamber at all times during the session.

2.3.2. Training with Periodic Signals (Sessions 1–20 and 26–30)

During training signals varied in the number (2 or 6) and base duration (250, 375, or 500 ms) of the 90 dB sound elements as illustrated in the upper panel of Fig. 1A. On each trial one of these six signals was randomly selected for presentation with equal probability. Signal presentations of a particular base duration consisted of 90 dB pulses inserted into a background level of 50 dB. At the end of the selected number of sound cycles, both levers were inserted into the box. If the rat made the correct response, a pellet of food was delivered; if the rat made the incorrect response, no pellet was delivered. For half of the rats a left-lever response was reinforced when the number of 90 dB sound cycles was two, and a right-lever response was reinforced when the number of sound cycles was six. The remaining rats had this response rule reversed. When either lever was pressed, both levers were immediately retracted. The 50 dB noise level was maintained during the intertrial interval (ITI) and was only terminated at the end of the session. ITIs were 5 s plus a geometrically distributed duration with a minimum of 0.1 s and a mean of 30 s. If an incorrect response had been made on the previous trial, the same signal was presented again on the next trial (correction procedure). A record was kept of the number of left and right responses following each of the trial types. All training sessions lasted 2 hours.

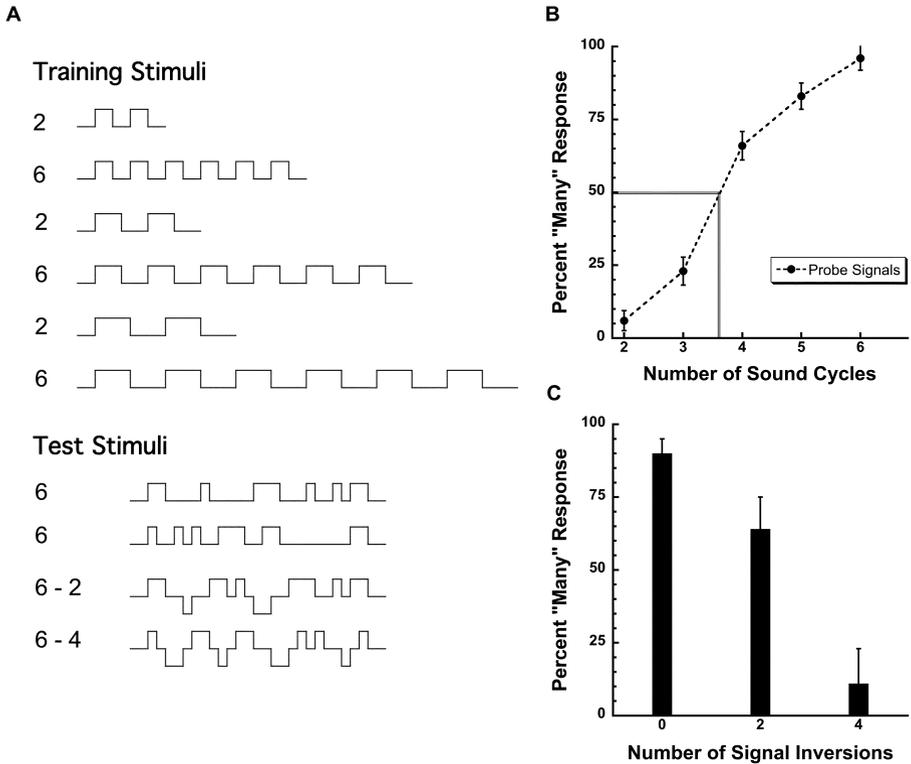


Figure 1. (A) Diagram of the temporal structure of the sound signal increments used during the training phase (top panel) and the combination of increments and decrements used during test phase (bottom panel). (B) Mean (\pm SE) percent 'many' response plotted as a function of the number of sound cycles. (C) Mean (\pm SE) percent 'many' response plotted as a function of the number of signal decrements (novel inversion) during testing.

3. Test Procedures and Results

3.1. Experiment 1. Testing with Periodic Signals (Sessions 21–25)

The six periodic standards were presented pseudo-randomly with equal probability on half the trials. Correct responses were reinforced and no correction trials were used. On the remaining trials, probe signals were presented pseudo-randomly with equal probability, and no responses were reinforced. Five periodic number probes held total signal duration constant at 4.0 s while the number of sound cycles varied between 2, 3, 4, 5, and 6. The probability of pressing the lever associated with six counts ('many' response) is plotted as a function of the number of signal increments (counts) in Fig. 1B. Sigmoidal functions were fit to the response functions of each subject using the Solver feature of Microsoft Excel. Next the Goalseek feature was used to determine three measures of number-bisection performance based on the fitted sigmoidal equation (see Lake et al., 2014 for details): the point of

subjective equality, or PSE (the number of sound cycles classified as ‘many’ on 50% of the trials); the difference limen, or DL (half the difference of the count classified as long on 75% of the trials and that classified as ‘many’ on 25% of the trials); and the Weber Fraction or WF (the DL divided by the PSE). These two latter measures index counting variability. The group means (\pm SD) for PSE, DL, and WF measures were 3.72 ± 0.09 , 0.67 ± 0.06 , and 0.18 ± 0.02 , respectively.

3.2. *Experiment 2. Testing with Novel Stimulus Inversions (Sessions 31–35)*

The conditions of training were the same as described for Sessions 21–25, except that during the unreinforced probe trials the number of sound cycles was held constant at six and the temporal structure of each signal was determined by randomly varying the 50 dB and 90 dB sound durations, constrained only by a minimum duration of 125 ms and the total duration of the signal which was held constant at 4.0 s. In addition, on a random half of the six-cycle probe trials 2 or 4 novel stimulus inversions were inserted. The novel stimulus inversions involved turning off the white noise stimulus for a period of time defined by the same temporal constraints used for the other probe trials. These stimulus inversions are referred to as the ‘6 minus 2’ and the ‘6 minus 4’ conditions given that the signal decrements (~ 0 dB noise) may be viewed as subtracting from the signal increments (90 dB noise) presented around a common baseline (50 dB noise) — as illustrated in the lower panel of Fig. 1A. The probability of pressing the lever associated with six counts (‘many’ response) is plotted as a function of the number of signal inversions in Fig. 1C. A single-factor, repeated measures ANOVA revealed a significant effect for the number of signal inversions, $F(2, 16) = 139.1$, $p < 0.0001$.

3.3. *Experiment 3. Duration of Signal Increments and Decrements (Sessions 36–40)*

Several mechanisms could account for the results of Experiment 2. Could the results be due to mere integration of the time the signal was present, or is it more closely related to the number of ‘on’ and ‘off’ events? To address this question, we asked if it is the length of the signal ‘increment’ or ‘decrement’ that matters or if it is instead the number of increments/decrements which might be added/subtracted regardless of the duration of the sequence element? In order to address this issue the temporal structure of each six-cycle trial’s stimulus sequence was determined by randomly varying the duration of the background sound level and all increments (sound-on) and decrements (sound-off) in its intensity. Variation in the duration of sequence elements was constrained only by a minimum duration of 200 ms for each element and the total duration of the signal. Individual six-cycle trials were classified according to (1) whether the mean duration of the signal increments was in the lowest or highest quartile and (2) whether the mean duration of the signal decrements was in the lowest or highest quartile. The probability of pressing the lever associated with six counts (‘many’ response) is plotted as a function of the lowest (L) and highest (H) quartiles for durations of signal increments (I) and

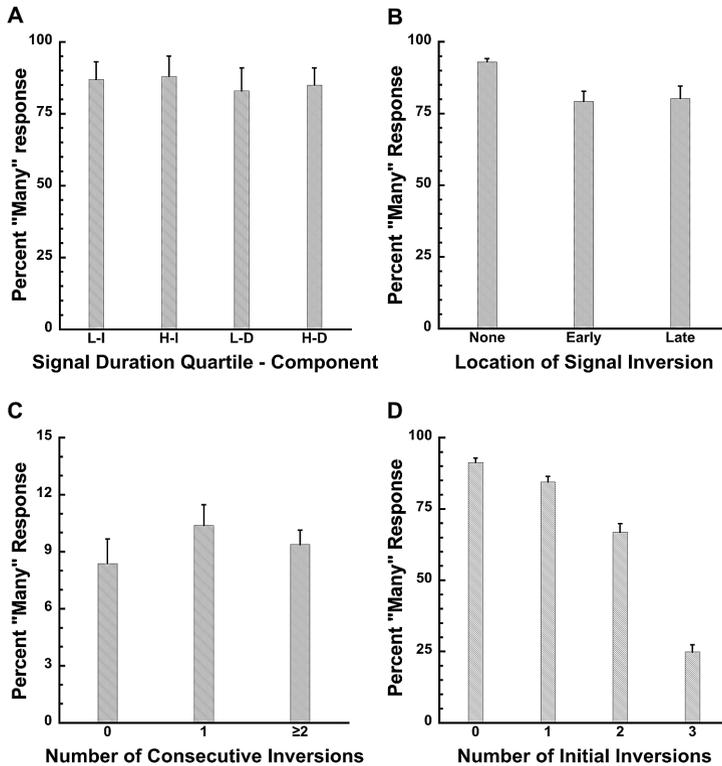


Figure 2. (A) Mean (\pm SE) percent 'many' response plotted as a function of the lowest (L) and highest (H) quartile for sound signal increments (I) and decrements (D) during testing. (B) Mean (\pm SE) percent 'many' response as a function of the location of a signal decrement (novel inversion) within a trial, i.e., during testing inversions could occur early or late within a trial or not at all. (C) Mean (\pm SE) percent 'many' response as a function of the number of consecutive sound signal decrements (novel inversions). (D) Mean (\pm SE) percent 'many' response as a function of the number of sound signal decrements (novel inversions) that occurred prior to the first increment.

decrements (D) in Fig. 2A. A single-factor, repeated measures ANOVA revealed no reliable effect of signal component duration, $F(3, 24) = 0.42$, $p > 0.1$, suggesting that the number of events rather than the integration of acoustic energy over time was the determining factor in the rats' choice behavior.

3.4. Experiment 4. Location of Novel Inversions: Early vs. Late Subtraction (Sessions 41–45)

Signal inversions may simply 'reset' the accumulation process rather than subtract an amount equal to a single count for each inversion (see Buhusi & Meck, 2000, 2002; Buhusi et al., 2002, 2005). If so, the position within the sequence of the final inversion would be expected to strongly influence responses. On average the final inversion would be expected to occur later in sequences with four inversions than

those with only two inversions. In order to investigate this possibility, we evaluated the effect of inversion location on six-cycle test trials containing a single novel signal inversions. Trials were classified according to whether the signal inversion onset occurred prior to or after the mid-point of the stimulus sequence. If signal inversions produce a complete resetting of the accumulation process, then an inversion presented late in the trial should have a greater effect than an inversion presented early in a trial. On the other hand, if the effect of signal inversions is due to a subtraction of a relatively fixed quantity/inversion from an ongoing accumulation, then the location of signal inversions within a stimulus sequence should have little effect. The probability of pressing the lever associated with six counts ('many' response) is plotted as a function of the occurrence and location (Early vs. Late) of a novel signal inversion during six-cycle test trials in Fig. 2B. A single-factor, repeated measures ANOVA revealed a significant effect of signal location, $F(2, 21) = 5.50$, $p < 0.05$. Fisher's Protected LSD tests indicated that both the Early and Late locations differed from the None condition (p 's < 0.05), but not from each other, $p > 0.05$.

3.5. Experiment 5. Multiple Consecutive Subtractions (Sessions 46–50)

Although signal inversions may result in a type of subtraction process, it is possible that they may be operating by only negating or masking the most recent signal increment and that earlier increments within the trial sequence are not accessible for subtraction. In order to determine whether it is possible for the counting system to implement multiple consecutive subtractions, six-cycle test trials containing four novel signal inversions were classified according to whether or not they contained 0, 1, or ≥ 2 consecutive inversions with no intervening signal increments. The probability of pressing the lever associated with six counts ('many' response) is plotted as a function of the number of consecutive novel signal inversions that occurred during six-cycle test trials in Fig. 2C. A single-factor, repeated measures ANOVA indicated that there were no reliable effects of the number of consecutive signal inversions, $F(2, 21) = 0.89$, $p > 0.05$, suggesting that consecutive subtractions with no intervening additions are possible.

3.6. Experiment 6. Negative Subtractions (Sessions 51–55)

Do you have to have some positive quantity, i.e., an increment — before subtraction is possible or can you build a deficit as long as there is an expectation of stimulus increments being presented? In order to investigate this possibility we presented 0, 1, 2, or 3 novel stimulus inversions (randomly selected with equal probability) prior to the presentation of any stimulus increments on six-cycle test trials. The probability of pressing the lever associated with six counts ('many' response) is plotted as a function of the initial number of novel stimulus inversions that occurred during six-cycle test trials in Fig. 2D. A single-factor, repeated measures ANOVA revealed a significant effect of the number of initial sound signal

inversions, $F(3, 28) = 167.84$, $p < 0.0001$. Fisher's Protected LSD post-hoc tests indicated that all comparisons were significant, $p < 0.05$, suggesting that it is possible for a deficit to be accumulated.

4. General Discussion

The present evidence for spontaneous subtraction can be accounted for by an analog-accumulation mechanism that is able to integrate stimuli with different signs (e.g., increments and decrements) in a manner similar to the simultaneous integration of time and number through the use of different mode switches and accumulators operated in parallel (e.g., Brannon & Roitman, 2003; Church & Broadbent, 1990; Meck, 1997; Meck & Church, 1983; Roberts, 1995). The finding that signal duration and location have no reliable effect on the outcome of the subtraction process supports the proposal that a 'count' may be represented by a fixed amount of time (with a mean and specified amount of variability) that is stable across a variety of signal parameters (Broadbent et al., 1993; Meck et al., 1985). In addition, the observation that the number of consecutive novel stimulus inversions had no effect on the outcome of the subtraction process indicates that signal increments and decrements are directly comparable and accessible for computation. Most importantly, the observation that the number of initial inversions were subtracted from subsequent signal increments suggests that there is a meaning to a zero 'accumulator reading' defined by the representation of both positive and negative values that can be combined on the same number line. This interpretation of the present results is in contrast to the proposal made by Wynn and Chiang (1998) who argue that human infants cannot represent zero. Nevertheless, these investigators consider their findings to be consistent with the accumulator model given the assumption that if the accumulator is activated it must represent a positive value — an assumption that overlooks the possible results of addition and subtraction operations, either within or across stimulus modalities for a variety of species (see Buhusi & Cordes, 2011; Church & Meck, 1984; Cordes et al., 2007; Kobayashi et al., 2004; Meck & Church, 1982a, b; Penney et al., 2000, 2008; Robinson & Ninowski, 2003; Sulkowski & Hauser, 2001).

Analog representations of stimulus magnitudes have been explored using 'mode-control' models of temporal integration as a guide for understanding non-symbolic counting and timing processes in animals, non-verbal infants, young children, and adults (see Allman et al., 2012; Brannon, 2002, 2004; Brannon et al., 2004; Clement & Droit-Volet, 2001; Dehaene et al., 1999; Droit-Volet et al., 2003; Gallistel & Gelman, 1992; Meck & Church, 1983; Meck et al., 1985; Wynn, 1995, 1998). The mode-control model posits that magnitude estimations of time and number are mediated by the same 'pacemaker/accumulator' system, but operated in different pulse accumulation modes (e.g., a *run* mode for time and an *event* mode for number). This unified model of temporal integration has become influential in

the debate surrounding the foundations of numerical thinking and the evidence for nonverbal counting ability in a variety of animals, including rats, monkeys, and human infants (e.g., Brannon & Roitman, 2003; Brannon & Terrace, 1998; Brannon et al., 2001; Breukelaar & Dalrymple-Alford, 1999; Broadbent et al., 1993; Church & Meck, 1984; Dehaene et al., 1999; Gallistel, 1990; Gallistel & Gelman, 1992; Grondin et al., 1999; Roberts, 1995; Roberts & Mitchell, 1994; Starkey & Cooper, 1980; Starkey et al., 1990; Strauss & Curtis, 1981; Whalen et al., 1999; Williams, 2012; Wynn, 1992, 1995, 1998; Wynn & Chiang, 1998).

Counting behavior is accounted for in the mode-control model by assuming that at the onset of a relevant stimulus pulses are directed into an accumulator so that they can be integrated over time. This is accomplished by a 'mode switch' that allows pulses to flow into the accumulator in one of three different modes depending on the nature of the stimulus (see Allman et al., 2012, 2014; Brannon & Roitman, 2003; Hinton & Meck, 1997; Meck, 1997; Meck & Church, 1983; Meck et al., 1985). In this model numerosity is represented by the linear magnitude of an internal variable (e.g., pulse accumulation), and it is this value that is remembered and entered into calculation. The mode-control model is assumed to explain counting when the switch is set to the *event* mode. In this condition discrete stimuli are marked by a fixed increment in the accumulator. It is this temporal integration process that represents the numerosity of events or objects and thus constitutes this model's proposed numeron, just as this same temporal integration process represents duration when pulses are gated through the switch in the *run* or *stop* modes. Evidence from previous experiments showing that this fixed increment in the accumulator is equal to approximately 200 ms (Meck & Church, 1983; Meck et al., 1985 — see Moore et al., 1997) and from the current Experiment 3 showing that the final numerical value representing the sequence of events is independent of the durations of the signals triggering the increments and decrements strongly suggests that the number of events, rather than the temporal integration of acoustic energy over time (Pedersen & Salomon, 1977; Valente et al., 2011), is the determining factor in these experimental paradigms.

The mode-control model provides a unified theory of counting and timing by positing the existence of an isomorphism between number and duration. The model incorporates the idea that the nervous system inverts the representational convention whereby numbers are used to represent linear magnitudes. Instead of using number to represent magnitude, it is proposed that the nervous system uses magnitude to represent number (see Carey, 2001; Gallistel & Gelman, 2000; Gelman & Cordes, 2001). This framework shares some similarity with the ATOM model ('A Theory Of Magnitude' — Walsh, 2003), which asserts that there is a single magnitude system, operational from birth and common to a variety of different species, that can develop into the apparent specializations we see for space, time and quantity. There is both behavioural evidence for this idea, as seen from studies showing interactions between numerosity, space, and temporal judgements (e.g., Agrillo &

Piffer, 2012; Burr et al., 2010a; Dormal et al., 2006, 2008, 2012b; Droit-Volet et al., 2003; Gilaie-Dotan et al., 2014; Roitman et al., 2005; Xu, 2003; Xu & Spelke, 2000; Xuan et al., 2007), as well as neuroimaging evidence showing overlapping areas responding to magnitude, time and numerosity judgements (see Buetti & Walsh, 2009; Dehaene & Brannon, 2010; Dehaene et al., 1999; Hayashi et al., 2013; Walsh, 2003). The mode-control model for duration and number differs from ATOM however, in that it does not argue for a single registration mechanism for all analog magnitudes, although there may be a common representation of these values at the level of decision-making (Meck, 1997; Meck et al., 2012). Beyond this descriptive framework the mode-control model provides a mechanism through which the relationship between temporal and numerical representations could operate in order to calculate rate and other amodal stimulus attributes (e.g., Brighouse et al., 2014; Church & Broadbent, 1990; Meck et al., 1984).

It is also possible to conceive of simple addition and subtraction within the structure of the mode-control model. In the latter case, it seems that a subtraction operation between two 'opposite' sensory representations (in this case, increments and decrements of intensity from a baseline value) may be a general processing strategy used by the brain to reach decisions and ultimately trigger behavior. In order to provide for subtraction, one would have to postulate an accumulation mechanism that is able to contrast information from different sensory inputs with opposite stimulus valences. This might involve separate counters for different types of events that are later combined at the level of the accumulator to perform the overall subtraction (or addition) process. Alternatively, the ability to add and subtract counts from a single accumulator may be sufficient to perform the types of arithmetic operations described here, but probably not the types of statistical inferences attributed to apes and potentially other animals (e.g., Rakoczy et al., 2014; Shi et al., 2013).

There is evidence to suggest that the use of such neural accumulation and comparison mechanisms develops in humans and other animals performing distinct perceptual tasks (e.g., Allman et al., 2012; Burr & Ross, 2008; Burr et al., 2010b; de Lafuente & Romo, 2003; Ditterich et al., 2003; Matell & Meck, 2004; Meck & N'Diaye, 2005; Romo & Salinas, 2003; Romo et al., 2003). Indeed amongst humans there is mixed evidence for the ability of young children to perform non-symbolic subtractions (e.g., Barth et al., 2006, 2008; Gilmore et al., 2007; Langer et al., 2003; Lipton & Spelke, 2003; Slaughter et al., 2006; Zur & Gelman, 2004). However beyond their importance to developmental research, the study of subtraction and the concept of zero and negative numbers has important clinical implications for the investigation of a number of different clinical conditions. Developmental dyscalculia, where individuals have severe difficulties with simple mathematical operations, has particular relevance as researchers try to disentangle whether difficulties stem from difficulties with individual's fundamental numerical abilities or from higher level mathematical abstractions (Butterworth, 2010). A paradigm

such as this, that can elicit spontaneous subtraction procedures through the use of inversions, could be of particular importance where traditional subtraction measures have found mixed results. Additionally other clinically relevant conditions such as down syndrome, Williams disorder, Autism and ADHD have all been associated with numerical difficulties (Chiang & Lin, 2007; Corbett et al., 2009) but these are often comorbid with language or attentional abnormalities. The current simple task yielding spontaneous subtraction may be better suited to investigation. Autism, in particular, has also been linked to temporal difficulties, further underlying the need for studies simultaneously considering temporal and numerical aspects of perception (Allman & Meck, 2012; Allman et al., 2011, 2012; Falter et al., 2012a, b; Kwakye et al., 2011; Szelag et al., 2004).

Although experience can shape an individual's perception, there are properties of the environment (e.g., time, space, and number) that are universal to all niches and hence have been incorporated into brain and behavior (Gallistel, 1989, 1990). These universals involve temporal-spatial sequences of events, where one of the fundamental perceptual operations is the grouping of successive events into higher-order patterns, an operation critical to the perception of language as well as rhythm and music (e.g., Aagten-Murphy et al., 2014; Agostino et al., 2008; de la Mora et al., 2013; Gu et al., 2011; Iversen et al., 2009; Schirmer, 2004). Perceptual grouping has long been thought to be governed by innate principles (Woodrow, 1909). Moreover, perceptual grouping for time, space, and number has been shown to be bootstrapped by abstract perceptual principles as reviewed by Iversen et al. (2008), Meck and Church (1982a, b), and Yoshida et al. (2010). The current work demonstrates that non-linguistic auditory sequences can be grouped together to form a representation of number — thus obeying the one-to-one, stable-order, and cardinality definitional criteria for counting proposed by Gelman and Gallistel (1978). Moreover, these sequences can be operated upon as a whole (see Taubert et al., 2011) in order to spontaneously subtract inversions (e.g., intensity decrements) after initially being trained to summate other events (e.g., intensity increments). Presumably similar results would be observed if the sensory attributes and/or direction of change of these elements and separating gaps or breaks were reversed (e.g., Buhusi & Meck, 2000, 2006; Buhusi et al., 2002, 2005; Fortin et al., 2009; Viau-Quesnel et al., 2014). Importantly, this same grouping of events was spontaneously processed both in terms of the total number of events and the total duration of the sequence without explicit training (Fernandes & Church, 1982; Meck & Church, 1983; Meck et al., 1985). This work demonstrates that these forms of perceptual grouping and arithmetic can be independent of explicit training in terms of how the auditory inversions should be handled and suggests that the observed results are evidence for perceptual grouping and basic arithmetic skills in rats, which may be present in other animals (e.g., Brannon et al., 2001; Patel et al., 2009).

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