Induced Alpha-band Oscillations Reflect Ratio-dependent Number Discrimination in the Infant Brain

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Abstract

■ Behavioral studies show that infants are capable of discriminating the number of objects or events in their environment, while also suggesting that number discrimination in infancy may be ratio-dependent. However, due to limitations of the dependent measures used with infant behavioral studies, the evidence for ratio dependence falls short of the vast psychophysical datasets that have established ratio dependence, and thus, adherence to Weber's Law in adults and nonhuman animals. We addressed this issue in two experiments that presented 7-month-old infants with familiar and novel numerosities while electroencephalogram measures of their brain activity were recorded. These data provide convergent evidence that the brains of 7-month-old infants detected numerical novelty. Alpha-band and theta-band oscillations both differed for novel and familiar numerical values. Most importantly, spectral power in the alpha band over midline and right posterior scalp sites was modulated by the ratio between the familiar and novel numerosities. Our findings provide neural evidence that numerical discrimination in infancy is ratio dependent and follows Weber's Law, thus indicating continuity of these cognitive processes over development. Results are also consistent with the idea that networks in the frontal and parietal cortices support ratio-dependent number discrimination in the first year of human life, consistent with what has been reported in neuroimaging studies in adults and older children. ■

INTRODUCTION

A wealth of behavioral research has revealed that infants represent approximate numbers well before they acquire language (e.g., Wood & Spelke, 2005b; Xu, Spelke, & Goddard, 2005; Brannon, Abbott, & Lutz, 2004; Lipton & Spelke, 2003, 2004; Xu & Spelke, 2000; Starkey & Cooper, 1980). Psychophysical numerical discrimination studies indicate that adults and children represent number as continuous mental magnitudes that are proportional to the numerosity being represented (see e.g., Brannon, 2006, for a review). As predicted by Weber's Law, which states that the ratio and not the absolute difference between two to-be-compared quantities determines their discriminability, accuracy and reaction times for adults and children comparing two numerosities are dependent on the ratio between the values rather than their absolute difference. Parallels between animal and human performance in numerosity discrimination tasks also suggest that the system for representing analogue magnitudes is evolutionarily continuous (e.g., Cantlon & Brannon, 2006; Hauser, Tsao, Garcia, & Spelke, 2003).

Behavioral studies in infants using visual habituation and head-turn paradigms suggest that the ratio between numerical values is also important for numerical discrimination in infancy. For example, when infants as young as 6 months of age are habituated to arrays that contain eight elements, they subsequently look longer at arrays with 16 elements (and vice versa), even when stimuli are controlled for total surface area and perimeter (Xu & Spelke, 2000). In contrast, using the same behavioral paradigm, 6-month-old infants appear to be unable to discriminate 8 from 12 dots, but by 9 months of age infants succeed at discriminating this 2:3 ratio contrast. However, such evidence is indirect because it is inferred by the pattern of successes and failures rather than by psychometric functions (Brannon, 2005; Xu et al., 2005; Lipton & Spelke, 2003, 2004; Xu & Spelke, 2000). In contrast, electrophysiological measures can provide graded responses in infants, and thus, can potentially provide data more analogous to the well-established reaction time and accuracy distance effects found when adults, children, and nonhuman animals make numerical comparisons (see Brannon, Libertus, Meck, & Woldorff, 2008 for the case of duration discrimination).

To date, little is known about the neural underpinnings of numerical representation in infancy. Although functional neuroimaging research suggests that the intraparietal sulcus, the region most heavily implicated in adult numerical cognition, is recruited when children as young as

4 years observe changes in the numerosity of visual arrays (Cantlon, Brannon, Carter, & Pelphrey, 2006), only two studies have examined the neural correlates of numerical processing in infants. In the most recent study, Izard, Dehaene-Lambertz, and Dehaene (2008) examined event-related potentials (ERPs) when 3-month-old infants saw changes in either the number of elements or the identity of the elements in a visual adaptation paradigm. Number changes, but not identity changes, elicited large ERP differences over right parietal scalp sites, whereas identity changes, but not number changes, elicited differences over occipito-temporal areas. These findings suggest an early differentiation of processing pathways that may correspond to the theorized ventral and dorsal visual processing streams (Ungerleider & Mishkin, 1982) and also indicate that, already at 3 months of age, parietal areas may contribute to numerical information processing.

A second study used the violation-of-expectation paradigm in combination with ERPs to investigate infants' neural response when detecting arithmetic errors (Berger, Tzur, & Posner, 2006). Infants were tested with a modified version of a behavioral paradigm developed by Wynn (1992), in which infants were presented with movies in which one or two toys were placed on a stage and were subsequently occluded by a screen. In an addition condition the infant watched as a second toy was placed behind the screen and in a subtraction condition the infant observed one of two occluded toys removed from behind the screen. After the addition or subtraction event, the screen was lowered to reveal the correct solution (e.g., two toys in the addition condition and one toy in the subtraction condition) or an incorrect solution (e.g., one toy in the addition condition or two toys in the subtraction condition). ERPs over midline frontal and central scalp sites showed an increased negative-polarity amplitude for incorrect as compared to correct solutions, an effect that is similar to modulations of the central negativity (Nc) that has been reported to be attention sensitive in infants (Reynolds & Richards, 2005). Secondly, power in the theta and alpha frequency band, time-locked to the presentation of the solution, was greater for the incorrect as compared to the correct arithmetic solution over fronto-central scalp sites. A similar pattern of ERP and oscillatory results was found in adults tested in a symbolic arithmetic error-detection task. Thus, these findings support Wynn's behavioral observation that infants can detect simple arithmetic errors and suggest that infants and adults may recruit similar error-detection processes when noticing mathematical violations. However, with respect to electroencephalogram (EEG) frequency analyses in other contexts, previous research has shown that adults and infants typically exhibit *decreases in alpha power* under conditions of *increased attention* (Sauseng, Klimesch, Schabus, & Doppelmayr, 2005; Stroganova, Orekhova, & Posikera, 1999; Klimesch, Doppelmayr, Russegger, Pachinger, & Schwaiger, 1998). Thus, it is unclear why

incorrect solutions led to *increases* in alpha power and to increases in looking time, both of which would typically be associated with increases in attention.

One prevalent component in ERP studies with infants is the Nc component (Quinn, Westerlund, & Nelson, 2006; Reynolds & Richards, 2005; de Haan & Nelson, 1997; Nelson & Collins, 1992; Courchesne, Ganz, & Norcia, 1981). Several previous studies on recognition memory in infants have found that the Nc amplitude decreases with increasing repetition of a stimulus or category of stimuli, with the decrease being most pronounced over frontal and central scalp sites (Wiebe et al., 2006; de Haan & Nelson, 1997, 1999; Nelson & Collins, 1992). Similarly, studies on emotion processing in infants have reported that the Nc amplitude over frontal and central electrodes is smaller for emotionally neutral prosody or for faces that draw less attention than for positive or negative emotional stimuli (Grossmann, Striano, & Friederici, 2005, 2006). Furthermore, Richards (2003) reported that the amplitude of the Nc component for familiar and novel stimuli elicited during periods of attention is larger than for the same stimuli during periods of inattention. Thus, collectively, ERP studies with infants suggest that this medium-latency negativity is a domain-general response whose overall amplitude may reflect heightened attention and/or increased novelty.

The goal of the present study was to seek electrophysiological correlates of numerical discrimination in 7-month-old infants and explicitly test these for ratio dependence. To this end, we recorded EEG activity while we familiarized 7-month-old infants to a given numerosity and then subsequently presented both the familiar numerosity and either one (Experiment 1) or two (Experiment 2) novel numerosities in pseudorandom order. In Experiment 1, the novel numerosity differed by a 1:2 ratio from the familiar value (8 and 16; see Figure 1 for a sample stimulus sequence); in Experiment 2, one novel numerosity differed by a 1:3 ratio and the other by a 1:2 ratio from the familiar numerosity (12, 36, and 18 or 24 depending on the familiarization condition). We predicted that the Nc ERP component and the alpha-band oscillatory activity would reflect differential processing of numerically novel compared with numerically familiar stimuli. Specifically, we expected to find that the Nc component would be greater and the power in the alpha-band oscillations would be reduced for novel compared with familiar stimuli. A second goal was to assess whether any neural correlate of numerical novelty was modulated by numerical ratio. We found that numerical novelty induced changes in both alpha-band and theta-band oscillations; contrary to our ERP prediction, however, the effect of novelty on the Nc component was only marginally significant. Moreover, we observed that the differential spectral alpha power for novel versus familiar numerosities was ratio dependent. This study thus provides the first within-subject

parametric demonstration that number discrimination in preverbal infants adheres to Weber's Law.

METHODS

Participants

Fifty infants with a mean age of 7 months (m) and 3 days (d) (range = 6 m 10 d to 7 m 27 d; 25 girls) participated. Ten of these infants participated in two conditions (see below) yielding 60 datasets. Data from 74 additional infants were discarded due to fussiness ($n = 19$), insufficient looking at the screen (i.e., less than 50% of familiarization or test trials) ($n = 35$), excessive noise in the data ($n = 12$), equipment failure ($n = 5$), parental interference ($n = 1$), premature removal of the cap ($n = 1$), or external interference ($n = 1$). These attrition rates are comparable to those in other EEG studies that use visual presentations with infants (e.g., Izard et al., 2008; Berger et al., 2006; Quinn et al., 2006).

Stimuli and Procedure

Parents gave written informed consent to a protocol approved by the Duke University Institutional Review Board. Infants sat in a high chair or on a parent's lap approximately 90 cm away from a computer screen. Soft music, not time-locked to the stimulus presentation, was played in the background to help infants remain calm. All infants were videotaped for later off-line coding of their looking behavior.

Participants were familiarized to one numerosity, for example, eight black dots randomly arranged on a white background, for 40 trials (Figure 1). Each stimulus was presented for 500 msec with a variable interstimulus interval (ISI) of 500–1000 msec. During familiarization, the average cumulative surface area for stimuli with the smaller and the larger number of elements was identical. On half of the trials, individual element size was equal, and on another half of the trials, cumulative perimeter was equated to avoid confounding such effects with number. The familiarization phase started off with a colorful attractor stimulus, which reappeared every 10 trials to maintain the infants' attention to the screen. Stimulus duration and ISI were not changed during the test phase. The attractor stimulus reappeared every 11 test trials. For test displays, density was equated between novel and familiar numerosities (0.02 objects/cm^2).

In Experiment 1, infants were familiarized to either 8 or 16 and tested with both numerosities in pseudorandom order. In Experiment 2, infants were familiarized
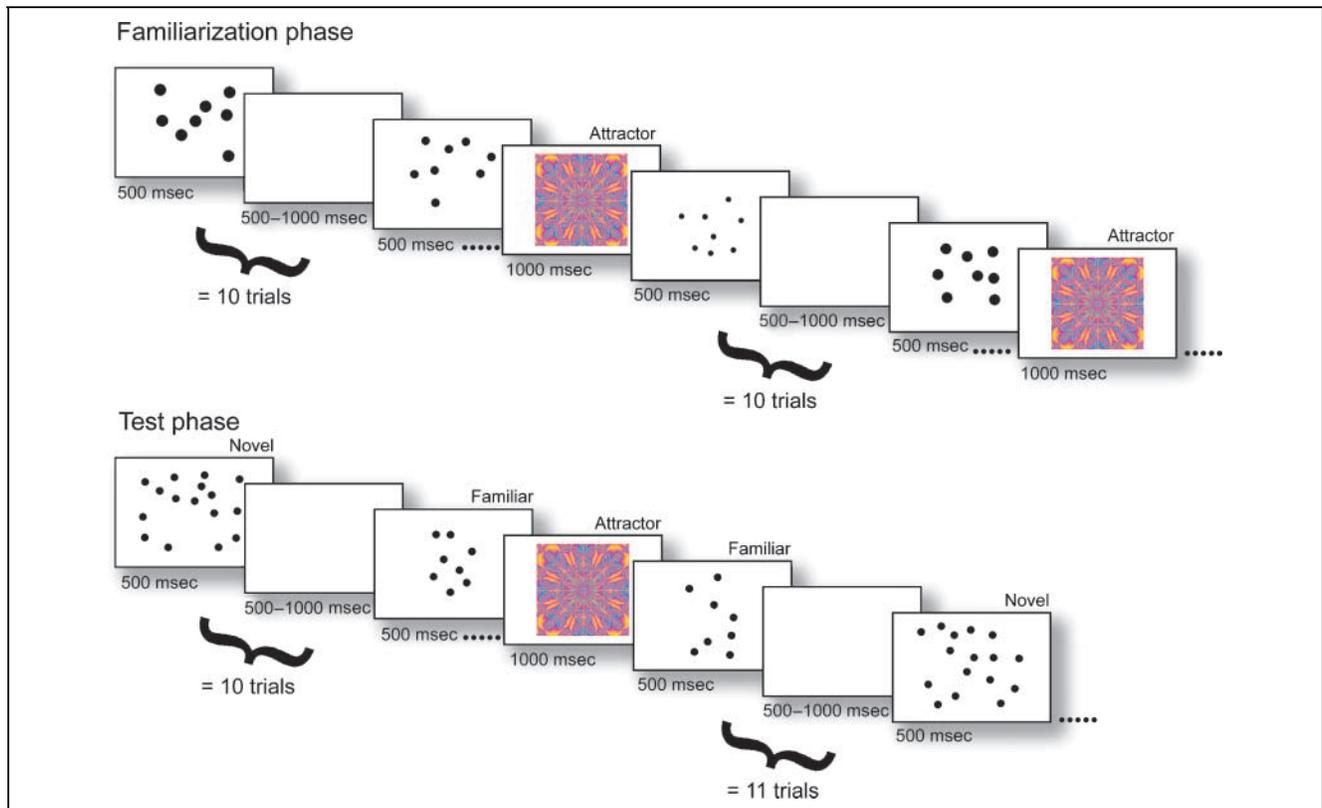

Figure 1. Experimental design. Infants were first familiarized to a given numerosity (e.g., 8 dots) and then tested with new images that contained novel and familiar numerosities (here: 8 and 16 dots). Each run consisted of a familiarization phase with 40 trials separated in blocks of 10 trials by a colorful attractor stimulus, and a test phase in which the familiar number of elements and either one (Experiment 1) or two (Experiment 2) novel numbers were presented in random order, with no more than three stimuli of the same numerosity occurring consecutively. Fifty percent of all test trials contained the familiar numerosity.

to 12 or 36 and tested with 12, 24, and 36 if they were familiarized to 12, or with 12, 18, and 36 if they were familiarized to 36. The middle value changed to maintain a 1:2 ratio between the familiar and novel numerosities. Again, test trials were presented in pseudorandom order to avoid anticipatory effects on any of the trials. In all our analyses, the first trial following each attractor stimulus was excluded, leaving a total of 36 possible familiarization trials and 20 possible test trials (Experiment 1, 10 familiar and 10 novel) or 40 possible test trials (Experiment 2, 20 familiar, 10 novel test trials for each ratio). An on-line observer coded the infant's looking behavior to the screen during the entire run. Twenty-five percent of the runs were coded off-line by another observer (interobserver reliability = 92.5%).

EEG Acquisition

Brain electrical activity was recorded using 19 tin electrodes placed according to the International 10–20 System in an elastic cap (Electrocap, Eaton, OH). Impedances were maintained as low as possible, aiming for under 10 kΩ. In most cases, simply filling the electrodes with gel and eliminating air bubbles was sufficient, but some very light abrading was used if necessary. Recordings were referenced to the right mastoid during acquisition and later algebraically re-referenced to an average of the right and left mastoids. The EEG was amplified with a gain of 150. A recording band pass of 0.01–100 Hz was used, and the EEG was digitized continuously at a rate of 500 Hz/channel onto disk. The recorded EEG was examined off-line (both visually and with computer algorithms) to reject those epochs with eye movements or other electrical artifacts in any of the channels. Trials in which the maximum or minimum amplitude exceeded ±250 μV in any channel were marked as artifacts and trials in which the peak-to-peak amplitude (difference between maximum and minimum amplitude over a 1400-msec time window) exceeded 1200 μV were excluded as most likely reflecting eye or other movement-related activity. Only trials in which the participant was looking to the screen were included in the analysis. On average, each infant that was included in the analysis contributed 26 familiarization trials (72%) and 13 test trials in Experiment 1 (6.9 novel, 6.6 familiar; 65% of all test trials) and 28 test trials in Experiment 2 (13.9 novel, 13.8 familiar; 70% of all test trials). Thus, there were approximately equal numbers of trials for familiar and novel numerosities in both experiments. Effects between 0 and 1000 msec poststimulus were analyzed.

ERP Analysis

The data from both experiments were selectively averaged for familiar and all novel test trials during the test phase, and then these averages were amplitude-calibrated using a standardization pulse of the system. Subsequently, the data were low-pass filtered using a 9-point running average, which filters out activity at and above 56 Hz at the 500-Hz sample rate used here. The recorded EEG was also high-pass filtered (>0.16 Hz) to remove low-frequency noise and drift, and low-pass filtered (<20 Hz) to remove high-frequency noise most likely caused by muscle activity. To analyze the effect of numerical novelty on infants' brain waves, we first baselined all data to the average amplitude of the last 100 msec before stimulus onset and then calculated a difference wave at all electrode sites by subtracting the ERP to numerically familiar test items from the ERP to numerically novel test items. Statistical analyses were performed over the mean amplitudes of the difference waves for the participants. Data were treated as independent measures even though a small subset of infants participated in more than one condition. In addition, data were excluded from statistical analyses if the amplitude of the difference wave exceeded two standard deviations above or below the mean. Analyses of the ERPs were guided by previous studies that reported effects of novelty over parietal, frontal, and central scalp sites (e.g., Quinn et al., 2006; Reynolds & Richards, 2005; de Haan & Nelson, 1997; Nelson & Collins, 1992; Courchesne et al., 1981). In line with these reports, we analyzed ERPs at nine electrodes along the frontal, central, and parietal midline and over the left and right hemispheres (F3, F4, Fz, C3, C4, Cz, P3, P4, Pz).

Frequency Analysis

The unfiltered EEG data were segmented, time-locked to the onset of familiar and novel test trials. Only trials in which the infants were looking at the screen and which were free of artifacts were included in the analysis. To assess which frequency bands might show effects of numerical novelty, we first band-pass-filtered the segmented EEG data for three frequency ranges that have been previously studied with infants of this age in other domains: theta 4–6 Hz (Orekhova, Stroganova, Posikera, & Elam, 2006), alpha 6–8 Hz (Stroganova et al., 1999), and gamma 21–55 Hz (Kaufman, Csibra, & Johnson, 2005). These frequency ranges for theta, alpha, and gamma activity in infants are thought to differ from the common ranges found in adults due to changes in EEG oscillatory patterns across development (Hudspeth & Pribram, 1992) and are defined based on functional similarity to adult oscillatory effects. Visual inspection suggested effects of numerical novelty only in the theta and the alpha frequency range. Thus, all subsequent analyses were performed on only these two frequency ranges.

To assess the effects of numerical novelty in the alpha and theta range more precisely, we filtered the original segmented data (without band-pass filtering) using a Butterworth Zero Phase Filter with 0.1 Hz as the low

cutoff and 20 Hz as the high cutoff. Next, we applied a fast Fourier transform (FFT) using a Hanning window with 10% tapering on each end and a resolution of 0.977 Hz. The magnitudes of FFT transformed data were then averaged separately for familiar and for novel tests trials, both combined across the two experiments as well as separately for each experiment to assess potential induced effects of numerical ratio. Statistical analyses were performed over the mean spectral power for the different trial types for each participant over a given frequency band.

RESULTS

Event-related Potentials

ERPs for novel and familiar numerosities revealed differences across a time range that included both an early positivity (200–300 msec poststimulus) and a medium-latency negativity (300–600 msec). Both time windows revealed a highly similar topographical distribution of the difference between novel and familiar numerosities, which consisted of a larger negativity for novel numerosities than for familiar numerosities, an effect that is consistent with an increase in portions of the attention-related Nc wave previously reported in infants (Reynolds & Richards, 2005). Thus, we collapsed both time windows for our statistical analyses.
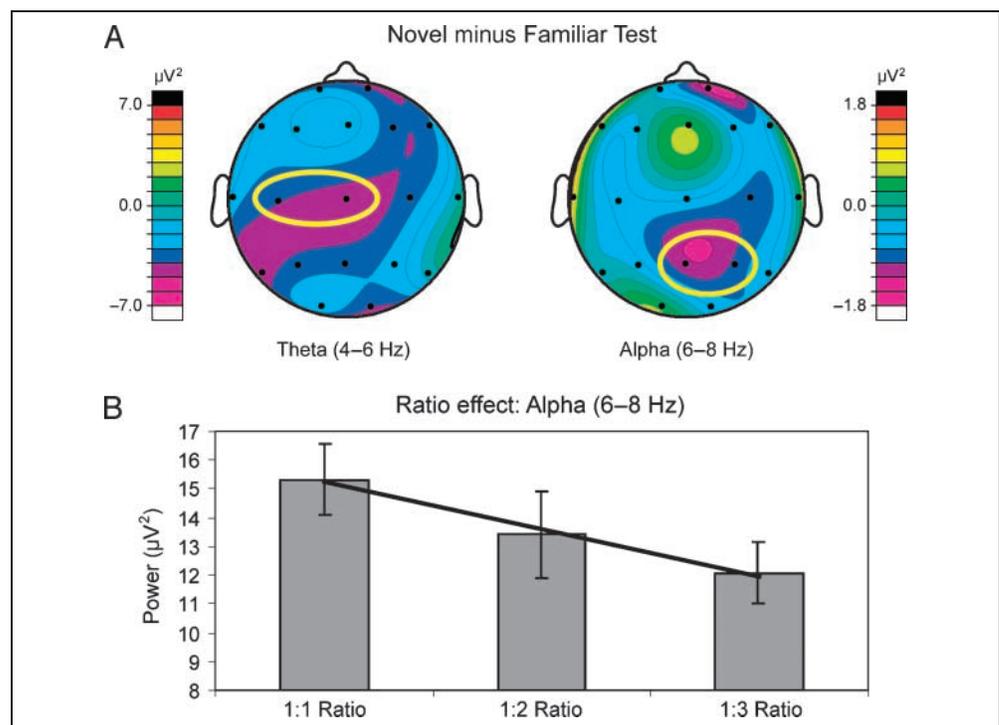
Given that our prediction was that the frontally distributed, negative-polarity Nc wave would be larger for novel than for familiar test trials, we conducted separate one-sample t tests comparing the mean amplitude, relative to zero, of the difference waves between novel and familiar test trials between 200 and 600 msec poststimulus over the nine scalp sites of interest. We found a trend toward a difference over the left frontal scalp at site F3 [$t(55) = 1.98, p = .05$, one-tailed; uncorrected for multiple comparisons]. None of the other channels showed any significant effects of numerical novelty (all ts < 0.66, ps > .26). An ANOVA with factors of experiment (Experiment 1 or 2) and familiarization condition (smaller or larger numerical value) analyzing the mean amplitude of the difference wave at electrode F3 showed no significant main effects or interactions [$F(1, 52)$ < 1.63, p > .21].

Frequency Results

Preliminary analysis (see Methods) suggested that the alpha band (for this age range: 6–8 Hz; Stroganova et al., 1999) and the theta band (4–6 Hz; Orekhova et al., 2006) might show effects of numerical novelty. Thus, we examined the spectral power in both frequency bands more closely using an FFT across the entire 1-sec time window following each stimulus onset. Across both experiments, we found significantly larger theta power for familiar than for novel numerosities over left central and midline central electrodes [paired t tests: site C3, $t(59) = 2.2, p < .04$; site Cz, $t(59) = 2.0, p < .05$]. In the alpha frequency range, familiar numerosities again

Figure 2. Spectral power in the theta and alpha frequency bands for novel and familiar test trials. (A) Topographical distribution of spectral power differences in the theta (4–6 Hz) and alpha frequency band (6–8 Hz) for novel minus familiar test trials across Experiments 1 and 2. Novel test trials elicited significantly less power than familiar test trials over left and midline central scalp sites for the theta band, and over midline and right parietal and central scalp sites for the alpha band. (Scalp sites with statistically significant differences are highlighted.) (B) Alpha power for test trials in Experiment 2, shown separately for familiar test trials (1:1 ratio), novel test trials that differed by a 1:2 ratio from the familiar ones, and novel test trials that differed by a 1:3 ratio from the familiar ones. A significant linear decrease in alpha power was found at midline parietal (Pz) and midline central (Cz) scalp sites, with familiar test trials eliciting the largest alpha power and novel test trials that differed by a 1:3 ratio from the familiar ones eliciting the smallest alpha power.

had more power than novel numerosities. However, in this case, significant differences were observed over right parietal and midline parietal electrodes [site P4: $t(59) = 2.1$; $p < .04$; site Pz: $t(59) = 2.5$; $p < .02$; see Figure 2A].

In Experiment 2, where two different novel numerical values were presented to each infant, we also examined both frequency ranges for potential ratio effects. We first determined the mean spectral power for familiar numerosities (1:1 ratio), for novel numerosities that differed by a 1:2 ratio from the familiar ones, and for novel numerosities that differed by a 1:3 ratio. For each frequency band, we then calculated linear regressions for each individual to determine the slope of the function relating trial type (1:1, 1:2, and 1:3 ratio) to spectral power. For the alpha frequency range, a one-sample t test revealed that the slopes were significantly smaller than zero at midline parietal and central electrodes [Pz: $t(29) = -2.6$, $p < .02$; Cz: $t(29) = -2.5$, $p < .02$; see Figure 2B].[1] Thus, spectral power in the alpha band decreased as the degree of numerical novelty increased. No such differences were found in the theta band. Furthermore, to assess whether there were differences in the spectral alpha power when the ratio was held constant at 1:2 and the absolute values of the numerosities was varied, we compared the spectral alpha power for novel and familiar test trials in Experiment 1 (1:2 ratio) and the 1:2 ratio condition of Experiment 2. A two-way ANOVA of mean spectral power with absolute value and trial type (novel vs. familiar) as factors showed no significant main effects of absolute numerosity value or interactions over any of the central or parietal scalp sites [$F(1, 57) < 0.671, p > .4$].

DISCUSSION

Our experiments provide convergent evidence for neural correlates of numerical discrimination in 7-month-old infants. We found that both theta-band (4–6 Hz) and alpha-band (6–8 Hz) oscillatory power differentiated novel and familiar numerosities across two experiments. For both frequency bands, spectral power was greater for familiar numerosities as compared to novel ones. Critically, the power in the alpha band, but not in the theta band, varied as a function of the numerical ratio. The larger the relative difference between numerosities (1:3 ratio vs. 1:2 ratio), the larger the difference in alpha power between novel and familiar numerosities. Moreover, as predicted by Weber's Law, the absolute difference between numerosities for a given ratio (1:2 ratio for Experiment 1 vs. Experiment 2) did not affect the alpha power. This is the first parametric within-subject demonstration of ratio dependency in numerical discrimination in infancy.

In contrast to the robust oscillatory effects that differentiated novel and familiar numerosities, our ERP analyses only revealed a trend for a larger negative-wave response over left frontal scalp sites for numerically novel compared to numerically familiar stimuli. It is not entirely clear why we did not obtain the same ERP effects over parietal areas that differentiated numerically novel and familiar values as found by Izard et al. (2008), that is, a larger posterior negativity for novel as compared to familiar numbers. However, there are a few noteworthy differences in the experimental paradigms used in Izard et al. versus in our study. First, Izard et al. used a visual oddball paradigm, whereas we used a familiarization paradigm in our study. Second, the stimulus durations differed (Izard et al.: 1500 msec; our study: 500 msec). Third, Izard et al. presented both novel numerosities and novel shapes, whereas we only varied numerosity. However, although the ERP effects differed in the two studies, the alpha-band numerical novelty and ratio effects we observed occurred over posterior scalp sites similar to the location of Izard et al.'s ERP effects. Thus, another possibility is that our ERP effects were not strong enough to produce statistically significant effects over parietal scalp sites, but that our oscillatory analyses were able to detect them. Finally, Izard et al. did not indicate any ratio effects. Although their study was not designed to examine ratio effects, they did, in fact, employ three different ratios and their data do not suggest any ratio modulation in the ERPs. It is conceivable that an analysis of their electrophysiological data in the frequency domain (as opposed to an ERP analysis) might similarly have revealed ratio dependence. Alternatively, it is possible that 3-month-old infants (vs. the 7-month-old infants used in our study) do not yet show sensitivity to numerical ratio.

We interpret the modulation of the alpha frequency range as a function of numerical ratio as likely reflecting variations in attention to numerosity as a function of novelty. This interpretation is consistent with previous research that has shown that adults and infants exhibit decreases in alpha power under conditions of increased attention even on a trial-by-trial basis (Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Sauseng et al., 2005; Stroganova et al., 1999; Klimesch et al., 1998). Thus, our findings in the alpha frequency range may reflect parametric increases in attention to the novel stimuli as a function of the degree of numerical novelty. In contrast, theta rhythm in infants has been found to increase under conditions that evoke emotional arousal (Kugler & Laub, 1971; Maulsby, 1971) and in states of anticipation such as during a "peek-a-boo" game (Orekhova, Stroganova, & Posikera, 1999). In the current study, it does not seem likely that infants were more aroused or had higher anticipatory effects to familiar numbers. In adults, theta synchronization is typically accompanied by alpha desynchronization and is thought to reflect increases in memory demands (Klimesch, 1999). Further investigation in the cognitive processes underlying changes in theta power—especially in infancy—thus seems necessary. For example, as mentioned in the Introduction, it is unclear why, in the context of arithmetic error detection, Berger et al. (2006) found both

alpha and theta power increases for incorrect solutions as compared to correct solutions for both infants and adults, and why under those circumstances increases in attention as measured by increases in looking time correlated with increases in alpha power. One possible explanation for these differences is that the authors employed the same frequency ranges for infants as for adults, which may not functionally correspond.

It is interesting to note that we found neural correlates for numerical novelty discrimination despite the fact that stimuli were presented very briefly to avoid eye movements and to be in keeping with prior visual EEG studies with infants (500 msec, intertrial interval of 500–1000 msec). Wood and Spelke (2005a), using behavioral measures, found that at 5 months of age infants required a presentation time of at least 1700 msec and an intertrial interval of 300 msec to discriminate a 1:2 ratio of sets of visually presented objects, at least as measured in a standard visual habituation paradigm. In order to succeed with shorter presentation durations, 5-month-olds required numerosities that differed by a 1:4 ratio. It is possible that this difference can be explained by the ability to extract numerical information from briefly presented visual arrays improving between 5 and 7 months of age. However, it is also possible that electrophysiological measures are more sensitive than looking time measures, at least for brief stimulus presentations (e.g., de Haan & Nelson, 1999).

In addition to providing a more robust neural correlate of numerical novelty, the frequency analysis revealed ratio dependence, which was not seen in the ERP data. This difference may result from different sensitivities of the two analyses. Although ERPs have higher temporal resolution for changes in neural activity, analyses of induced frequency changes that are extracted trial-to-trial can detect oscillatory neural activity that is not consistently phase-locked and/or time-locked to the events and may therefore be missed in the ERPs or evoked oscillatory analyses (Tallon-Baudry & Bertrand, 1999). Future studies should also consider time–frequency analyses (e.g., moving-window FFTs or wavelet analyses) to include information about neural processes from both domains. Unfortunately, the fast presentation of stimuli in our study did not permit such analyses for the lower frequencies that showed sensitivity to numerical novelty here.

One potential explanation consistent with the spatial distribution of our ERP and frequency analyses is that ERP differences over frontal areas are elicited by numerical novelty but actually reflect domain-general processes. Such an explanation would fit with the generality of the infant Nc-ERP effects that have been found in a broad range of domains reviewed earlier. In contrast, the spectral power differences in the alpha band might reflect number-specific processing in parietal areas. Such an interpretation is consistent with numerous findings in adult humans and older children implicating parietal

cortex in number processing. And more specifically, it is consistent with recent findings by Izard et al. (2008) that directly compared a numerical and nonnumerical change in a stream of stimuli and found that only number changes yielded parietal ERP differences in 3-month-old infants. However, increases in alpha power—mostly over posterior scalp sites—have also been found in a variety of conditions that lead to increases in attention (Sauseng et al., 2005; Klimesch et al., 1998; Başar, Schürmann, Başar-Eroglu, & Karakaş, 1997). Therefore, the effects of numerical novelty in the alpha frequency band here may alternatively reflect domain-general processes as well. Regardless, our results provide strong evidence for numerical discrimination abilities in infants at 7 months of age and that these abilities adhere to Weber's Law.

It is important to note that our experimental design does not allow us to directly address the issue of number-specific neural correlates because we did not compare a numerical and a nonnumerical condition. Nevertheless, the electrophysiological differences we found to the numerically novel test stimuli relative to the numerically familiar stimuli can only be the result of the infants' ability to discriminate novel and familiar numerosities, given that our stimulus controls ruled out the contribution of perceptual variables such as cumulative area or element size. Thus, although our results do necessarily reflect a brain response due to the numerical attributes of the stimuli, they do not necessarily constitute neural correlates in the infant that are specific to number processing.

Conclusions

Our study reveals convergent evidence from induced theta-band and alpha-band oscillations for numerical discrimination in 7-month-old infants. The power of induced theta- and alpha-band oscillations differentiated between novel and familiar numerosities over central and posterior areas, respectively, with the modulations in alpha-band activity being proportional to the ratio between the novel and familiar numerosities. The graded effect of numerical ratio on the alpha-band oscillations is predicted by Weber's Law and provides the most direct evidence to date that infants use an analogue magnitude system for representing approximate numerosities that are common to adults, older children, and nonhuman animals.

Note

1. To test whether our ratio effect in the alpha band was due to a larger number of test trials for familiar than for novel numbers, we repeated our analyses using only half of the familiar test trials. Even with equal numbers of trials in all three conditions (1:1, 1:2, and 1:3), we found a significant ratio effect at the same electrode locations [Pz: $t(29) = -2.5, p < .02$; Cz: $t(29) = -2.5, p < .02$].

REFERENCES

Başar, E., Schürmann, M., Başar-Eroglu, C., & Karakaş, S. (1997). Alpha oscillations in brain functioning: An integrative theory. *International Journal of Psychophysiology, 26,* 5–29.

Berger, A., Tzur, G., & Posner, M. I. (2006). Infant brains detect arithmetic errors. *Proceedings of the National Academy of Sciences, U.S.A., 103,* 12649–12653.

Brannon, E. M. (2005). The independence of language and mathematical reasoning. *Proceedings of the National Academy of Sciences, U.S.A., 102,* 3177–3178.

Brannon, E. M. (2006). The representation of numerical magnitude. *Current Opinion in Neurobiology, 16,* 222–229.

Brannon, E. M., Abbott, S., & Lutz, D. J. (2004). Number bias for the discrimination of large visual sets in infancy. *Cognition, 93,* B59–B68.

Brannon, E. M., Libertus, M. E., Meck, W. H., & Woldorff, M. G. (2008). Electrophysiological measures of time processing in infants and adult brains: Weber's law holds. *Journal of Cognitive Neuroscience, 20,* 193–203.

Cantlon, J. F., & Brannon, E. M. (2006). Shared system for ordering small and large numbers in monkeys and humans. *Psychological Science, 17,* 401–406.

Cantlon, J. F., Brannon, E. M., Carter, E. J., & Pelphrey, K. A. (2006). Functional imaging of numerical processing in adults and 4-y-old children. *PLoS Biology, 4,* e125.

Courchesne, E., Ganz, L., & Norcia, A. M. (1981). Event-related brain potentials to human faces in infants. *Child Development, 52,* 804–811.

de Haan, M., & Nelson, C. A. (1997). Recognition of the mother's face by six-month-old infants: A neurobehavioral study. *Child Development, 68,* 187–210.

de Haan, M., & Nelson, C. A. (1999). Brain activity differentiates face and object processing in 6-month-old infants. *Developmental Psychology, 35,* 1113–1121.

Grossmann, T., Striano, T., & Friederici, A. D. (2005). Infants' electric brain responses to emotional prosody. *NeuroReport, 16,* 1825–1828.

Grossmann, T., Striano, T., & Friederici, A. D. (2006). Crossmodal integration of emotional information from face and voice in the infant brain. *Developmental Science, 9,* 309–315.

Hauser, M. D., Tsao, F., Garcia, P., & Spelke, E. S. (2003). Evolutionary foundations of number: Spontaneous representation of numerical magnitudes by cotton-top tamarins. *Proceedings of the Royal Society of London, Series B, Biological Sciences, 270,* 1441–1446.

Hudspeth, W. J., & Pribram, K. H. (1992). Psychophysiological indices of cerebral maturation. *International Journal of Psychophysiology, 12,* 19–29.

Izard, V., Dehaene-Lambertz, G., & Dehaene, S. (2008). Distinct cerebral pathways for object identity and number in human infants. *PLoS Biology, 6,* e11.

Kaufman, J., Csibra, G., & Johnson, M. H. (2005). Oscillatory activity in the infant brain reflects object maintenance. *Proceedings of the National Academy of Sciences, U.S.A., 102,* 15271–15274.

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: A review and analysis. *Brain Research, Brain Research Reviews, 29,* 169–195.

Klimesch, W., Doppelmayr, M., Russegger, H., Pachinger, T., & Schwaiger, J. (1998). Induced alpha band power changes in the human EEG and attention. *Neuroscience Letters, 244,* 73–76.

Kugler, J., & Laub, M. (1971). "Puppet show" theta rhythm. *Electroencephalography and Clinical Neurophysiology, 31,* 532–533.

Lipton, J. S., & Spelke, E. S. (2003). Origins of number sense. Large-number discrimination in human infants. *Psychological Science, 14,* 396–401.

Lipton, J. S., & Spelke, E. S. (2004). Discrimination of large and small numerosities by human infants. *Infancy, 5,* 271–290.

Maulsby, R. L. (1971). An illustration of emotionally evoked theta rhythm in infancy: Hedonic hypersynchrony. *Electroencephalography and Clinical Neurophysiology, 31,* 157–165.

Nelson, C. A., & Collins, P. F. (1992). Neural and behavioral correlates of visual recognition memory in 4- and 8-month-old infants. *Brain and Cognition, 19,* 105–121.

Orekhova, E. V., Stroganova, T. A., & Posikera, I. N. (1999). Theta synchronization during sustained anticipatory attention in infants over the second half of the first year of life. *International Journal of Psychophysiology, 32,* 151–172.

Orekhova, E. V., Stroganova, T. A., Posikera, I. N., & Elam, M. (2006). EEG theta rhythm in infants and preschool children. *Clinical Neurophysiology, 117,* 1047–1062.

Quinn, P. C., Westerlund, A., & Nelson, C. A. (2006). Neural markers of categorization in 6-month-old infants. *Psychological Science, 17,* 59–66.

Reynolds, G. D., & Richards, J. E. (2005). Familiarization, attention, and recognition memory in infancy: An event-related potential and cortical source localization study. *Developmental Psychology, 41,* 598–615.

Richards, J. E. (2003). Attention affects the recognition of briefly presented visual stimuli in infants: An ERP study. *Developmental Science, 6,* 312–328.

Sauseng, P., Klimesch, W., Schabus, M., & Doppelmayr, M. (2005). Fronto-parietal EEG coherence in theta and upper alpha reflect central executive functions of working memory. *International Journal of Psychophysiology, 57,* 97–103.

Starkey, P., & Cooper, R. G., Jr. (1980). Perception of numbers by human infants. *Science, 210,* 1033–1035.

Stroganova, T. A., Orekhova, E. V., & Posikera, I. N. (1999). EEG alpha rhythm in infants. *Clinical Neurophysiology, 110,* 997–1012.

Tallon-Baudry, C., & Bertrand, O. (1999). Oscillatory gamma activity in humans and its role in object representation. *Trends in Cognitive Sciences, 3,* 151–162.

Thut, G., Nietzel, A., Brandt, S. A., & Pascual-Leone, A. (2006). Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts

visual target detection. *Journal of Neuroscience, 26,* 9494–9502.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge, MA: MIT Press.

Wiebe, S. A., Cheatham, C. L., Lukowski, A. F., Haight, J. C., Muehleck, A. J., & Bauer, P. J. (2006). Infants' ERP responses to novel and familiar stimuli change over time: Implications for novelty detection and memory. *Infancy, 9,* 21–44.

Wood, J. N., & Spelke, E. S. (2005a). Chronometric studies of numerical cognition in five-month-old infants. *Cognition, 97,* 23–39.

Wood, J. N., & Spelke, E. S. (2005b). Infants' enumeration of actions: Numerical discrimination and its signature limits. *Developmental Science, 8,* 173–181.

Wynn, K. (1992). Addition and subtraction by human infants. *Nature, 358,* 749–750.

Xu, F., & Spelke, E. S. (2000). Large number discrimination in 6-month-old infants. *Cognition, 74,* B1–B11.

Xu, F., Spelke, E. S., & Goddard, S. (2005). Number sense in human infants. *Developmental Science, 8,* 88–101.