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Adaptation Affects Both High and Low (Subitized) Numbers Under Conditions of High Attentional Load

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Abstract

It has recently been reported that, like most sensory systems, numerosity is subject to adaptation. However, the effect seemed to be limited to numerosity estimation outside the subitizing range. In this study we show that low numbers, clearly in the subitizing range, are adaptable under conditions of high attentional load. These results support the idea that numerosity is detected by a perceptual mechanism that operates over the entire range of numbers, supplemented by an attention-based system for small numbers (subitizing).

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Keywords

Numerosity, subitizing, adaptation, attention

1. Introduction

Most adult humans can count. However, we also share an approximate non-verbal system with infants and other animals: a direct visual sense of number. When verbal counting is prevented, we can still see and estimate the numerosity of large sets of items, although with a margin of error (Whalen *et al.*, 1999). This error increases with increasing set size, following Weber's law (Ross, 2003; Whalen *et al.*, 1999), a common feature of perceptual processes. And like all primary sensory properties, numerosity is susceptible to adaptation: the prolonged exposure to a more numerous visual stimulus makes the current stimulus appear less numerous, and *vice versa* (Burr and Ross, 2008).

A debate has recently flared up over whether number is sensed directly, as proposed by Burr and Ross (2008), or estimated indirectly from other visual properties, such as texture density. Durgin (Durgin, 1995, 2008; Durgin and Proffitt, 1996) has

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made a strong case that number perception, and particularly number aftereffects, depend on *texture density*: ‘rather than requiring that the visual system jump right to a numeric representation, density aftereffects can be explained by earlier visual processes. It is possible to represent a correlate of density as something like statistical kurtosis in the visual image and this may be evaluated at various spatial scales’.

However, this notion contrasts strongly with much recent evidence, both in non-human primates (Nieder, 2005) and in humans (Piazza *et al.*, 2004) for the existence of neural circuitry specialized for number. There is also a good deal of psychophysical evidence that number perception is independent of texture density, such as the fact that joining dots to make bar-bells strongly reduces apparent numerosity, without affecting texture density (He *et al.*, 2009). And there is direct evidence that under conditions of conflict, numerosity can be extracted independently of texture density (Ross and Burr, 2010). However, there has been no clear demonstration to date that *adaptation* of number can occur independently from that to density.

The perception of small sets of items (up to 4 or 5) is thought to involve a system that is at least partially separate from estimation termed ‘subitizing’ (from the Latin *subitus* meaning immediately). Enumeration in this range is immediate and error-free (Kaufman *et al.*, 1949), and much evidence (Revkin *et al.*, 2008) suggests that naming numbers in the subitizing range involves processes distinct from those used in estimation. Recent evidence has shown that subitizing is particularly dependent on attention, and is highly compromised both with the ‘attentional blink’ (Shapiro *et al.*, 1997) paradigm (Egeth *et al.*, 2008; Olivers and Watson, 2008; Xu and Liu, 2008) and with dual-task paradigms (Railo *et al.*, 2008; Vetter *et al.*, 2008).

We have recently shown that both dual-task and attentional-blink paradigms affect precision performance (Weber Fraction) in the subitizing range far more than in a higher range (Burr *et al.*, 2010). Under attentional load, precision in the subitizing range deteriorated considerably to approach that of the higher estimation range. The results imply that two systems are involved with numerosity. However, we do not believe that the two number ranges are processed by completely independent mechanisms. We suggested that there may exist a pre-attentive estimation mechanism operating over the entire range of numbers, both large and small, and that this system is supplemented by an additional attentive mechanism with very limited capacity, capable of attending to up to about four items: the attentive mechanism makes performance virtually perfect over this low range (Burr *et al.*, 2010).

In this study we test directly this hypothesis by measuring adaptation to numerosity under demanding attentional load conditions. We show (confirming the original study of Burr and Ross (2008)) that under normal conditions adaptation has little effect in the low subitizing range. However, during dual-task conditions that require attention, adaptation affects both the estimation and the subitizing ranges.

2. Methods

The stimuli were presented in a dimly lit room on a 15-inch Macintosh monitor with 1440×900 resolution at refresh rate of 60 Hz and mean luminance of 60 cd/m^2 , and viewed binocularly by subjects from 57 cm. Stimuli were generated and presented under Matlab 7.6 using PsychToolbox routines (Brainard, 1997).

Three subjects with normal or corrected-to-normal vision participated in this study, two authors and one naïve to the goals of the study (all male, mean age 26). The experiment used a dual-task paradigm: subjects first performed a difficult conjunction task, then a numerosity judgment (see Fig. 1). The stimuli for the primary task comprised 4 centrally positioned colored squares, each subtending 1° of visual angle, presented concurrently with the numerosity matching task (lasting the entire duration of both test and probe). The squares could be arranged in eight different color combinations. If two green squares fell along the right-sloping diagonal *or* two yellow squares fell along the left diagonal, the stimulus was a target. In the single-task condition, the conjunction stimulus was presented as before, but subjects were instructed to ignore them.

The *test* stimulus for the secondary task (numerosity comparison) was a cloud of non-overlapping dots (diameter 10 arcmin), half white and half black at 90% contrast. The dots were constrained to fall within a virtual circle of 4° visual angle, and were always separated from each other by at least 12 arcmin. The

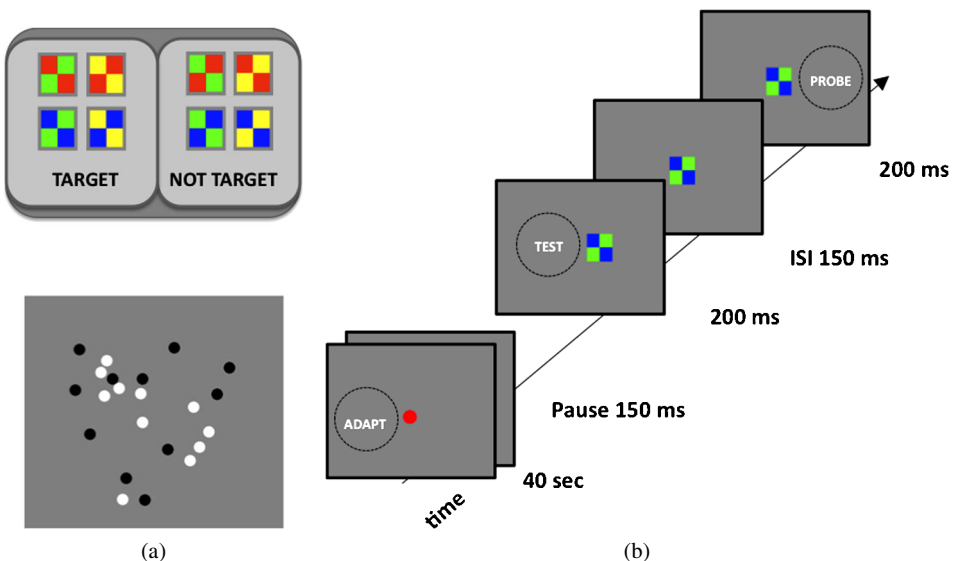


Figure 1. (a) Illustrations of primary (upper) and secondary (lower) stimuli. Primary stimuli were classed as targets if there were two green squares along the right-to-left diagonal *or* two yellow squares along the left-to-right diagonal. (b) Trial sequence: after adaptation (40 s on first trial, 6 s thereafter) to 200 dots, the *test*-stimulus was presented in the adapt region (200 ms); after 150 ms inter stimulus interval, the *probe* was displayed in the opposite field (200 ms). The colored squares remained on for 550 ms. This figure is published in color in the online version.

adaptation and probe stimuli were similar to the test, with the probe comprising 3, 6, 12 or 24 dots (depending on adaptation condition), and the *adaptor* 200 dots.

Each session started with 40 s of the adaptor presented 6° left of fixation; in subsequent trials it appeared for only 6 s (top-up adaptation). 150 ms after the adaptor disappeared, the test appeared for 200 ms in the same position as the adaptor, and the primary task (colored-squares) in the centre of the screen for 550 ms. 150 ms after the test was extinguished, a probe stimulus was presented for 200 ms, 6° right of fixation. The probe was also a dot pattern, similar to the test, with numerosity 3, 6, 12, 24 dots depending on condition. In the dual-task condition, subjects were required first to report whether the central stimulus was a target (by appropriate mouse-click), then respond whether the test or probe appeared to be more numerous. All subjects were about 90% correct on the conjunction task, with no differences between conditions: responses were recorded to the number task only if the response to the conjunction task was correct. In the no-load condition, subjects performed only the numerosity task.

The number of dots in the test was initially equal to the probe, then varied from trial to trial depending on subject response, with numerosity determined by the QUEST algorithm (Watson and Pelli, 1983), and with parameters initial numerosity = probe numerosity, standard deviation = 0.5 log-units; beta = 3.5; epsilon = 0.01; gamma = 0. To determine the numerosity of the next trial, the algorithm estimated the point of subjective equality (PSE) after each trial, then perturbed that with a random number drawn from a Gaussian distribution of standard deviation 0.15 log-units. At the end of each session, data were analyzed separately for each subject and condition. The proportions of trials where the test appeared more numerous than the probe was plotted against test numerosity and fitted with cumulative Gaussian functions like those of Fig. 2, yielding estimates of PSEs (median of psychometric function) and precision (standard deviation).

Statistical testing was performed by bootstrapped sign test of the whole procedure that led to the particular measure. For example, to test whether adaptation had a significant effect in the single task condition at $N = 6$, we calculated for each subject the PSE in that condition with a sample of data (with replacement, equal to the number of trials), and computed the average across subjects. The same was done for the no-adaptation single-task condition. The process was reiterated 10 000 times, counting which was the higher average on each reiteration. The proportion of times when the non-adapted condition had a higher mean than the adapted condition is the significance value.

For each subject there were two adaptation conditions, two attention conditions and 4 numerosities, yielding 16 conditions for each subject (with about sixty trials for each condition). The conditions were blocked into separate sessions, two sessions per condition, with order of conditions randomized between subjects. There was always a considerable pause (hours) between the adapted and non-adapted conditions to ensure that the effects did not carry over.

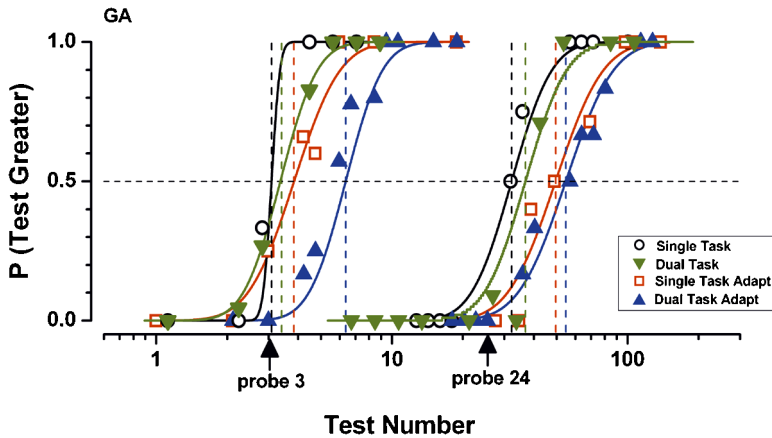


Figure 2. Example psychometric functions for subject GA for two numerosities (3 and 24) and four conditions. In all cases the proportion of times the subject reported the *test* to be more numerous than the probe (fixed at 3 or 24 dots) is plotted as a function of *test* number. The various conditions are indicated by the colors described in the legend. The effect of adaptation was far greater in the dual-task than in the single-task condition at low, but not high numerosities. This figure is published in color in the online version.

3. Results

Figure 2 shows sample psychometric functions for 1 subject, for three relevant conditions at two numerosities. At the highest numerosity measured (24 dots), the PSE in the no-adapt, single-task condition was 32, close to the veridical value of 24. After adaptation to 200 dots, 50 dots were required to match to 24, implying that the apparent numerosity of stimuli in the adapted region was greatly reduced. The result in the dual-task condition was also similar (54 dots). However, the pattern of results in for probe numerosity of three (subitizing range) was quite different. In the single-task condition, adaptation had only a weak effect (PSE = 3.8, compared with no-adapted PSE = 3.4), while in the dual-task condition the adaptation was as strong as for larger numerosities (PSE = 6.3).

The results of all subjects are summarized in Fig. 3, both for the three individual subjects (symbols) and averages across subjects (bars). The ordinate reports the ratio of the PSE of the particular condition to that of the baseline for that numerosity (single-task, no adaptation). A value of one means that the adaptation and/or dual-task had no effect, greater than one means that the apparent numerosity of the test was *reduced* by that factor (so the test numerosity was increased to obtain the match). As the example psychometric functions of Fig. 2 show, attentional load affected adaptation in the subitizing range. In the single-task condition, adaptation affected perceived numerosity for large numerosities (Bootstrap *t*-test with: $N(6)$ $p = 0.03$; $N(12$ and $24)$ $p < 0.01$), but very little effect where $N = 3$ ($p = 0.38$). However, under attentional load the effect of the adaptation increased considerably for low numbers to 40%, nearly as much as for the large numbers (50%). The effects of attentional-load by itself are shown by the black right-slanting bars. For

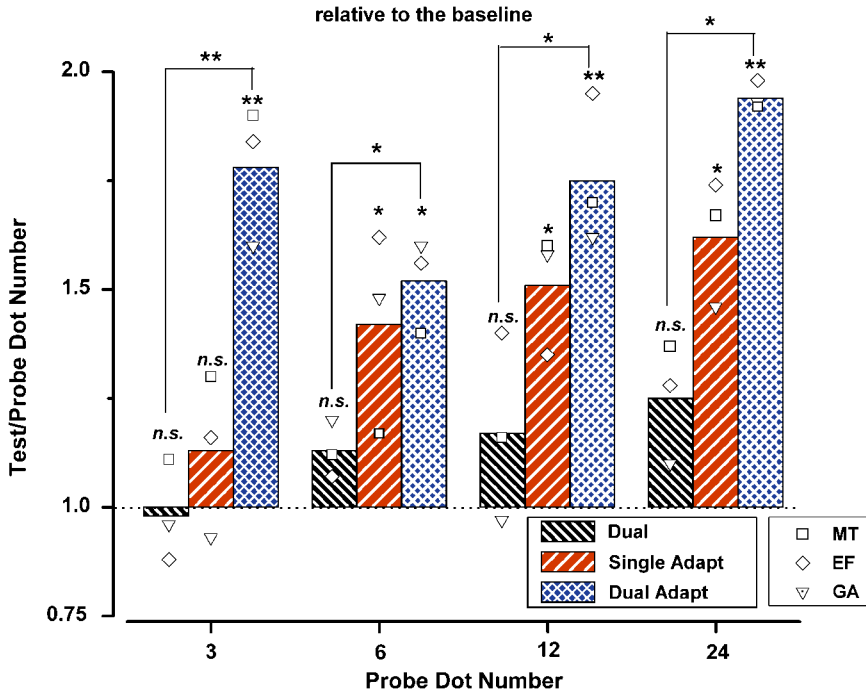


Figure 3. Effect of attention and adaptation on number estimation. Symbols report individual results (EF is the naïve subject); bars indicate averages of the three subjects. All data show the PSE for that particular condition divided by the PSE for the single-task, no-adaptation condition at that numerosity. Values greater than unity mean that the perceived numerosity of the *test* is proportionally less than of the probe. (Color coding: right-slanting black — dual task, no adaptation; red left-slanting — adaptation, single-task; blue cross-hatched — adaptation, dual-task.) The values of all conditions were tested for statistical difference from 1 by bootstrap sign-test (see methods), and the result reported by the symbols above each bar: *n.s.* $p > 0.05$; * $p < 0.05$; ** $p < 0.01$. This figure is published in color in the online version.

low number ($n = 3$), the double-task by itself had very little effect, but at higher numerosities it caused a slight underestimation, by about 25% at $N = 24$.

Figure 4 reports the geometric means of Weber Fraction against numerosity for all four conditions. Note that there are four rather than three conditions here, as the Weber fraction for the baseline is also shown. As previously reported, the strongest effects of attentional-load were in the subitizing range: there the Weber Fraction increases from 7% in the no-load condition to 16% in the double-task, while for the larger ranges it remains about in the order of 22–24% irrespective of attentional demand. The only significant effect of attentional load was in the subitizing range (see *t*-tests in figure caption), agreeing with our previous study (Burr *et al.*, 2010).

4. Discussion

In our previous study (Burr *et al.*, 2010), we presented evidence that subitizing depends strongly on attentional resources, whereas estimation of larger numbers

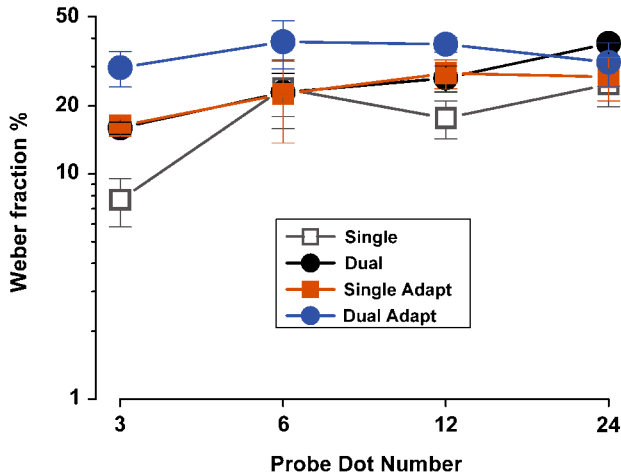


Figure 4. Mean Weber Fraction ($std/tested\ number$): color-coding as Fig. 3, with the single-task no-adaptation condition shown by open symbols. The strongest effects of attentional load were for the low numbers. T -tests between single and dual (non-adapted conditions) revealed significant effects only for the smallest numerosity: $N(3)$: $t = 3.93$, $p = 0.017$; $N(6)$: $t = 0.10$, $p = 0.92$; $N(12)$: $t = 1.84$, $p = 0.14$; $N(24)$: $t = 2.33$, $p = 0.09$. This figure is published in color in the online version.

was much less affected. We suggested that an estimation mechanism senses number directly over all ranges of numbers, but the low subitizing range benefit from an additional attention based mechanism. A direct prediction of this idea was that under conditions of high attentional load, the low subitizing range should also be strongly susceptible to visual adaptation. Our results verify this prediction, showing very strong effects of adaptation in the subitizing range in high-load, dual-task conditions, but very little in the single-task condition. Attention also affected adaptation of larger numbers, but the effects were much weaker. We also showed that precision was affected by attention more in the subitizing than estimation range, supporting our previous study (Burr *et al.*, 2010) and those of others (Egeth *et al.*, 2008; Juan *et al.*, 2000; Olivers and Watson, 2008; Railo *et al.*, 2008; Vetter *et al.*, 2008; Xu and Liu, 2008).

There is a long-standing debate regarding the possible existence of two neural systems for number processing — one precise and dedicated to numbers of items less than three/four and another one approximate system, dedicated to large sets (Feigenson *et al.*, 2004). On the other hand, that the estimation mechanism operates over both large and small number ranges is consistent with fMRI studies suggesting that the two ranges share common mechanisms (Piazza *et al.*, 2002). It is also consistent with more recent studies of neural correlates of visual enumeration under different attentional load (Vetter *et al.*, 2010), showing that the temporal-parietal junction (rTPJ), an area implicated in stimulus-driven attention (Corbetta and Shulman, 2002), responds to small numbers only in conditions of low attentional load, suggesting that this area could be the neural substrate for the attention-assisted boost in number-naming performance in the subitizing range.

Evoked potential studies in humans have also provided evidence for separate neural mechanisms for the subitizing and estimation ranges. For example, Hyde and Spelke (2009) have demonstrated that an early (N1) component is modulated by absolute number with small, but not large, number arrays, while a later component (P2p) is modulated by the ratio between arrays for small but not large numbers. Most interestingly, under dual-task conditions, the late component P2p is also modulated by small, as well as large numbers (Hyde and Wood, in press), suggesting that under these conditions, where the subitizing system is rendered ineffective, the estimation system continues to function, and dominates the evoked response.

Single-unit physiology (Nieder *et al.*, 2002) and behavioral data (Nieder and Miller, 2004) of macaque monkeys also suggest that estimation mechanisms work over both large and small number ranges. Two classes of number neurons have been described in monkeys: neurons in areas IPS with overlapping log-normal tuning curves each tuned to a specific number (Nieder, 2005); and a different type of neuron in area LIP, which responds in a graded manner to number, some maximally to large numbers some to small (Roitman *et al.*, 2007). These neurons have clearly defined receptive fields, and have been suggested as being the site of adaptation to numerosity.

We (Burr *et al.*, 2010) have previously shown that attentional load affects the capacity to estimate number most in the subitizing range, causing resolution thresholds to increase to the levels of estimation of larger numbers. We suggested that this implicated the existence of two separate mechanisms: one working over the entire range of numerosity (including subitizing), assisted by an attentional-based system of subitizing that operated for small numbers, no more than about four. One system, subitizing, is an exact and robust system, highly resistant to change by processes such as adaptation. However, during very demanding dual-task conditions, the attentional-based subitizing system cannot operate, and even this range is subject to adaptation.

That even very small numbers — as low as 3 — are subject to adaptation is very clear evidence that numerosity is adaptable directly, as these low numbers of items do not create patterns that can be considered ‘texture’ (usually considered to comprise an uncountable number of elements). Thus we conclude that, contrary to the claim of Durgin (2008), the number sense itself is subject to direct adaptation, like all other primary sensory attributes.

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