Counting on the motor system: Rapid action planning reveals the format- and magnitude-dependent extraction of numerical quantity

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Symbolic numbers (e.g., "2") acquire their meaning by becoming linked to the core nonsymbolic quantities they represent (e.g., two items). However, the extent to which symbolic and nonsymbolic information converges onto the same internal core representations of quantity remains a point of considerable debate. As nearly all previous work on this topic has employed perceptual tasks requiring the conscious reporting of numerical magnitudes, here we question the extent to which numerical processing via the visual–motor system might shed further light on the fundamental basis of how different number formats are encoded. We show, using a rapid reaching task and a detailed analysis of initial arm trajectories, that there are key differences in how the quantity information extracted from symbolic Arabic numerals and nonsymbolic collections of discrete items are used to guide action planning. In particular, we found that the magnitude derived from discrete dots resulted in movements being biased by an amount directly proportional to the actual quantities presented whereas the magnitude derived from numerals resulted in movements being biased only by the relative (e.g., larger than) quantities presented. In addition, we found that initial motor plans were more sensitive to changes in numerical quantity within small (1–3) than large (5–15) number ranges, irrespective of their format (dots or numerals). In light of previous work, our visual–motor results clearly show that the processing of numerical quantity information is both format and magnitude dependent.

Introduction

From clocks to costs to calendars, numbers pervade our daily life. Central to human cognition (and many of our technical and mathematical achievements, see Ansari, 2008; Dehaene, 1997) is our ability to

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accurately represent collections of items (e.g., three items) as abstract numerical symbols (e.g., "3"). One well-accepted view, perhaps inspired by the tremendous ease with which we transition between different numerical formats, argues that the core quantity derived from a number must be independent of its format (for reviews, see Ansari, 2008; Nieder & Dehaene, 2009; Piazza, 2010). Under this view, the number symbol "3," the word "three," and a visual display containing three items would all map onto the common underlying number sense of "three-ness." This intuitive notion has prompted the development of several influential models exploring how this convergent process might occur at the level of neurons (Dehaene & Changeux, 1993; Verguts & Fias, 2004), and findings from human behavior and neuroimaging showing, respectively, similar reaction times and similar patterns of brain activity elicited by different numerical formats of the same magnitude, offer compelling support for such models (Buckley & Gillman, 1974; Eger et al., 2009; Gallistel & Gelman, 2000; Moyer & Landauer, 1967; Piazza, Pinel, Le Bihan, & Dehaene, 2007). However, other theorists argue that neither these similar patterns of behavior nor brain activity are necessarily indicative of a format-independent representation of number (for review, see Cohen Kadosh & Walsh, 2009; for data, see Shuman & Kanwisher, 2004). (Note that when we discuss format-related differences in numerical processing we refer to the difference between symbolic and nonsymbolic formats rather than the different symbolic notations of numerical magnitude, as in Cohen Kadosh & Walsh, 2009). Recent evidence showing that selective brain areas are recruited depending on the numerical format of the display (He, Zuo, Chen, & Humphreys, 2013) offers particularly compelling support for the notion that the coding of numerical magnitude in the brain is instead highly format dependent.

A second dimension along which researchers studying numerical cognition can have dividing opinions is whether the processing of small numbers (e.g., less than four) and large numbers (e.g., five and greater) rely upon a common underlying numerical estimation mechanism. Again, evidence here is mixed, with some perceptual studies suggesting that the numerical estimation of small and large numbers relies on a single estimation procedure governed by Weber's law (Dehaene, 2007; Dehaene & Changeux, 1993; Gallistel & Gelman, 1991; Izard & Dehaene, 2008; Whalen, Gallistel, & Gelman, 1999), in which the sensitivity of numerosity discrimination is determined only by the ratio between numbers. By contrast, other research has shown dramatic differences in perceptual performance across the two number ranges in ways that are poorly accounted for by Weber's law (Feigenson, Dehaene, & Spelke, 2004; Revkin, Piazza, Izard, Cohen, & Dehaene, 2008; Trick & Pylyshyn, 1994, see also below).

Further complicating these above distinctions is the well-documented observation that the dimensions of format (nonsymbolic vs. symbolic) and number range (small vs. large) strongly interact. Specifically, a large body of findings, spanning multiple research fields, shows that humans (and other animals) possess an ability to immediately and precisely enumerate small quantities of items (usually four or less). Depending on the experimental paradigm, this specialized ability has been referred to as subitizing (Kaufman, Lord, Reese, & Volkmann, 1949), object tracking (Pylyshyn & Storm, 1988), or parallel individuation (Feigenson et al., 2004) and is thought to strictly apply to small number magnitudes represented by collections of real (nonsymbolic) items. Importantly, with collections of items having more than four objects and for magnitudes expressed symbolically (e.g., the numeral 5), numerical processing is thought to rely upon a separate approximate number system (for reviews, see Hyde, 2011; Piazza, 2010).

It is worth recognizing that nearly all previous work studying the effects of numerical format and magnitude, with a few notable exceptions like studies in nonverbal infants (e.g., Feigenson & Carey, 2005) and nonhuman primates (e.g., Hauser, MacNeilage, & Ware, 1996), has implemented purely visual–perceptual tasks in which participants are explicitly required to count, compare, track or recall the numerical magnitudes presented and in which their responses are measured via discrete measurements (e.g., key presses, verbal reports). Rather than restricting investigations of numerical processing to highly visual–perceptual tasks that require conscious reports, one particularly intriguing possibility is that the fundamental basis of the representation of numerical format and magnitude in the brain can also be probed by capitalizing on the strong action-associations humans form with numbers. From a behavioral perspective, we use numbers to guide both our long-term decisions and our moment-to-moment actions; for example, clocks and calendars are meaningful only in the sense that they may remind us to perform some action at a specific time on a specific day; the ability to calculate financial costs is relevant only if it is used to guide our future behavior (e.g., whether or not to purchase an item). Notably, the intimate link between number and action is not merely semantic but one that appears to be reflected in the cortical organization of the primate brain: parietal brain areas that represent numerical quantity and related processes are close to and often overlapping with the brain regions that support movement planning-related processes (Knops, Thirion, Hubbard, Michel, & Dehaene, 2009; e.g., Nieder & Dehaene, 2009; Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002; Walsh, 2003). Thus, the ways in which magnitude information is both used and cortically represented appear to be directly yoked to the planning of actions and behavior. This appealing notion has been explored across a variety of behavioral tasks showing that, in certain cases, the execution of movements (reaching and/or grasping) can be indirectly influenced by magnitude information presented during the task (e.g., Andres, Ostry, Nicol, & Paus, 2008; Fischer & Campens, 2009; Lindemann, Abolafia, Girardi, & Bekkering, 2007; Song & Nakayama, 2008).

We recently examined the direct links between action planning and nonsymbolic numerical processing by developing a novel behavioral task to determine how the number of potential targets influences rapid-reaching movements (see Gallivan et al., 2011). In this manual aiming task, subjects are forced to initiate speeded arm movements toward multiple potential targets before one of the targets is cued for action. Interestingly, we found that initial reach trajectories were increasingly biased toward the side of the target display containing more potential targets. Importantly, however, the presentation of more than four targets had no further effects on the spatial bias of initial reach trajectories. Despite the visuomotor system operating on a time scale faster than that used in perceptual discrimination, the capacity limit of four targets for reaching is very similar to the bottleneck often reported in a wide range of perceptual tasks when subjects are required to count, track, or recall collections of visually presented objects (e.g., Kaufman et al., 1949; Luck & Vogel, 1997; Pylyshyn & Storm, 1988; Revkin et al., 2008). This previous work suggests that the processes of action planning, as revealed through time-evolving reach movements, can yield direct insights into the fundamental basis of how quantity information is represented in the brain.

In consideration of ongoing debates concerning the format-dependent versus -independent and small versus large processing of number, here we implemented a novel version of our rapid reaching task to probe the underlying mechanisms that support the representation of number in the brain. The current study comprises two experiments, each of which has two experimental groups. The first experiment had two primary objectives. The first of these, explored in one group of subjects, was to replicate our previous work (Chapman et al., 2010a; Gallivan et al., 2011) showing that rapid reaches are sensitive to the magnitude of a small collection of items (hereafter referred to as nonsymbolic magnitude or dots) and to see if, under identical timing constraints (requiring very rapid magnitude processing), this sensitivity would also extend to small magnitudes expressed by Arabic numerals (hereafter referred to as symbolic magnitude or numerals). The second objective of the first experiment, explored in a separate group of subjects, was to see how both nonsymbolic and symbolic magnitude information would affect reaching behavior when participants were given an additional 500 ms of processing time prior to initiating a rapid reach movement. Overall, the goal of the first experiment was to provide a preliminary exploration of the effect of numerical format on rapid reaching and see how planning-related processes might be influenced by the time available for processing symbolic and nonsymbolic magnitudes.

Using the results from the first experiment to mitigate processing time differences across number formats, the second experiment was designed to address the two major debates in the literature on numerical processing. First, can reaching behavior reveal whether numerical magnitude processing is format dependent versus independent? Second, can it reveal whether the processing of small numbers is different than the processing of large numbers? To this end, in Experiment 2, two separate groups of participants were instructed to plan reaching movements based on cue displays containing dots or numerals that were either within the small number range (1–3; first group) or large number range (5–15; second group). If Arabic numerals yield the same magnitude information as their dot counterparts, then reaching performance on dot and numeral trials should be near identical. If, however, behavior substantially differs across these two formats, then it would indicate that the extraction of quantity information from number symbols fundamentally differs from the extraction of quantity information from sets of items. Likewise, if reaches performed towards displays with smaller magnitudes are different than those performed towards large magnitudes, then it might indicate a dedicated mechanism for the processing of small magnitudes. Importantly, in order to rule out the possibility that any differences between small and large number ranges might simply reflect Weber's law (whereby judgments become increasingly less precise with increasing magnitudes) the same target ratios in the dot and numeral cue displays were maintained across both small and large number ranges.

Materials and methods

Participants

A total of 117 right-handed participants took part in this study (29 in the Experiment 1 [E1] immediate group; 28 in the E1 delay group; 30 in the Experiment 2 [E2] small number group; and 30 in the E2 large number group). Handedness was determined by the Edinburgh handedness questionnaire (Oldfield, 1971).

All subjects had normal or corrected-to-normal vision, and were recruited from the University of Western Ontario (London, Ontario, Canada). Informed consent was obtained in accordance with procedures approved by the University's Psychology Review Ethics Board and consistent with the Declaration of Helsinki. Stringent exclusion criteria ensured that only participants who performed the task with sufficient speed and accuracy (see General methods information below) were included for analysis: E1-immediate, $N = 20$ (after nine excluded), five males, average age: 22.4 years; E1-delay, $N = 19$ (after nine excluded), 12 males, average age: 21.6 years; E2-small, $N = 22$ (after eight excluded), nine males, average age: 19.3 years; and E2-large, $N = 17$ (after 13 excluded), eight males, average age: 21.4 years. Each testing session for a participant took $\sim$ 1.5 hours. See also Supplementary information.

Overview of experiments

An important consideration we needed to address was whether different numerical formats require different amounts of cognitive processing time—regardless of whether they eventually arrive at a common representation in the brain (see Cohen Kadosh & Walsh, 2009). Although the processing delays inherent in the physical apprehension of a numerical symbol or a collection of items are not themselves of particular interest to researchers in numerical cognition, designing experimental paradigms that account for these processing delays is necessary for answering the bigger question of whether the representation of numerical quantity in the brain is format dependent or independent.

As such, E1 consisted of two experimental groups that performed trials differing only in timing. The first group, E1-immediate, was required to initiate a reach movement as soon as a cue display appeared (0-ms delay). The second group, E1-delay, was provided with a 500-ms preview of the cue display prior to being instructed to initiate a reach movement. We implemented a 500-ms delay interval because our recent work shows that it provides enough processing time in which to override differences in low-level visual features of cue displays (Wood et al., 2011) and because previous work in numerical cognition shows that numerical symbols most strongly influence behavior after 500 ms of processing (Fischer, Castel, Dodd, & Pratt, 2003). In both E1-immediate and E1-delay the cue displays contained either dots or numerals of small quantities (zero, one or two hollow circles on dot displays and 0, 1, or 2 Arabic numerals on numeral displays). E2 used a procedure that was identical to the delay trials from E1 except that we explored quantities within both the small and large number range. The E2-small group were presented with dot and numeral cue displays consisting of values 1, 2, and 3 whereas the E2-large group were presented with dot and numeral cue displays consisting of values 5, 10, and 15.

General methods information

We recorded rapid reach movements (index finger of right hand at sampling rate of 150 Hz, OPTOTRAK) from participants as they reached to a touch screen (40-cm reach distance, 32-in. screen at 1024 $\times$ 768 pixel resolution, 60-Hz refresh rate). Participants began each trial with their right index finger pressing a button at the starting location. Following presentation of a fixation cross (1000–2000 ms), Arabic numerals or dot targets (unfilled circles), in separate blocks of trials, were displayed on the left, right, or both sides of the touch screen. In the E1-immediate group, a beep cuing subjects to initiate a reach occurred simultaneously with the cue-display onset (0-ms delay). Since reaction times for this group were $\sim$ 235 ms (see Supplemental material for full analysis), this meant they had $\sim$ 235 ms to process the cue prior to reach onset. For the E1-delay, E2-small, and E2-large groups, the beep cuing them to initiate a reach occurred 500 ms after cue-display onset. For the E1-delay group, reaction times were $\sim$ 235 ms and for both the E2 groups, reaction times were $\sim$ 230 ms (see Supplemental material for full analysis), meaning that with the 500-ms delay we introduced, these groups had $\sim$ 730–735 ms total time to process the cue prior to reach onset. Upon initiation of a reach to touch the screen with their finger (within 325 ms of the beep cue) and the start button's release, the dot and numeral displays were briefly ($\sim$17 ms) replaced by a blank white screen and then replaced with a dot display where one of the target circles was filled in with black. Subjects had to correct their trajectory in flight and touch the screen at the location of the filled target (within 425 ms). Critically, in the numeral blocks (as well as dot blocks), when the initial display was replaced with a dot display, there was direct correspondence between the initial magnitude and the subsequent number of dots. That is, if the cue display had, for example, 1 (or one dot) on the left and 2 (or two dots) on the right then the target display would have one dot on the left and two on the right. Thus, the only difference between numeral and dot trials was the format of the quantity information presented in the initial cue display. Importantly, all targets in the target display always had an equal probability of filling in. As such, in both dot and numeral blocks, optimal performance required consideration of the initial quantity information contained in the cue display during movement planning. See Figure 1 and supplemental video for timing details.

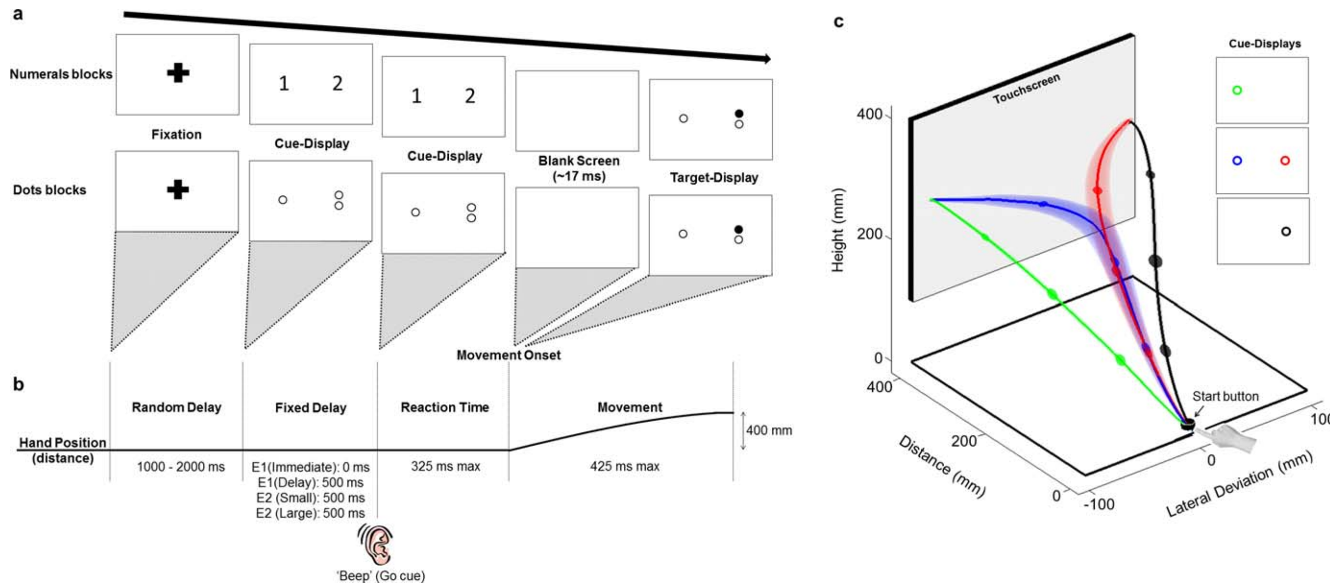

Figure 1. Illustration of the task (a), timing (b), and subjects' average arm trajectory (c). (a) Display sequence for a single trial in numeral (see top) and dot (see below) blocks. Note, in the E1-immediate group the beep cuing subject to initiate a reach occurred simultaneously with the cue-display onset (0-ms delay), while in the E1-delay group and E2-small and E2-large groups, the beep cuing them to initiate a reach occurred 500 ms after the cue-display onset. Critically, in the numeral blocks, when the initial display was replaced with a dot display, there was direct correspondence between the initial numeral magnitude and the subsequent number of dots. As such, the only difference between numeral and dot trials was the format of the quantity information in the initial cue display. All targets in the target display always had an equal probability of filling in. The diagram (b) below the displays in (a) illustrates the linkage between the participant's movement and the onset of the target display. (c) The three-dimensional view of the experimental setup shows reach trajectories for example dot displays (shown at right) averaged across 20 subjects from the immediate group in E1. Baseline trials (single target) are shown for illustrative purposes only and are analyzed in the Supplemental material. When targets appeared on both the left and the right, the cue could be on either side of the display; in the examples shown here, the color coding indicates the side of the display on which the cue appeared. Shaded areas around the darker trajectories (traces) represent average standard errors; the darkened ovals indicate 25%, 50%, and 75% of movement distance, and their size is proportional to the velocity in the *x*, *y*, and *z* dimensions (colors are for purposes of illustration only).

To ensure rapid and accurate movements, participants received performance feedback on the touch screen following each trial. There were four possible types of errors which caused the following text to be displayed on the touch screen: "Too Early" (if the start button was released before 100 ms had elapsed; this aborted the trial), "Time Out" (if the start button was not released within 325 ms following the beep cue; this aborted the trial), "Too Slow" (if the screen was not touched within 425 ms of button-release), or "Miss" (if subjects did not touch within a 6 cm $\times$ 6 cm box centered on the final target). "Good" was displayed on trials without errors. Trials that were too early, time out, or miss were removed from analysis, as were the slowest too slow trials (slowest 5% across all participants in an experiment). The remaining good and too slow trials were therefore analyzed. A participant was excluded if, after this trial removal, they had less than four analyzable trials in each experimental condition (i.e., for every target display for both dot and numeral trials, see Materials and methods). See the Supplemental material for information about trial and participant screening.

General analysis information

We were specifically interested in the movements planned in response to the cue display, since this is the only point in the trial sequence where the dot and numeral trials differed. Therefore, to isolate a measure of the reach response that was governed only by viewing of the cue display (and not contaminated by changes in the display encountered at reach onset), we focused our analysis on the trajectory deviation observed at 100 ms post-reach onset (corresponding to $\sim$70 mm of reach distance in all experiments). Since the target display did not actually appear until $\sim$ 17 ms after the onset of the movement (due to the blank screen refresh of the monitor) this means that our analysis was actually centered on early trajectory differences arising at $\sim$ 83 ms following target-display onset. This particular time point was chosen for analysis because it precedes the time in which sensory processing associated with the display change can possibly affect the movement trajectory. At the neural level, it takes ~ 90 ms for a change in visual information to even reach visuomotor structures in posterior parietal cortex (e.g., Mulliken, Musallam, & Andersen, 2008), one of the first sites where visual information can actually start to affect goal-directed action. In addition, at the behavioral level, the delay in involuntary motor corrections in response to changes in visual stimuli (including in-flight trajectory corrections) is around 110–150 ms (e.g., Brenner & Smeets, 1997; Day & Lyon, 2000; Franklin & Wolpert, 2008; Saijo, Murakami, Nishida, & Gomi, 2005), explaining why the early portion of a rapid reach movement is ballistic and based only on visual information accumulated prior to reach onset. In sum, an analysis of movement trajectories at 100 ms post-reach onset will only reveal biases in the initial motor plan based on the cue display and cannot reflect changes in the display that occur at reach onset.

Experiment 1 methods

Participants performed 12 experimental blocks with 48 trials per block. The block type alternated between dot and numeral blocks such that each block type appeared six times. The first block type was counterbalanced across participants and the first block of each type was used as training and was not included in analysis (this yielded 240 analyzed dot and numeral trials each, see the Supplemental material for additional information regarding trial and participant screening).

Experiment 1 analyses

To characterize the bias induced by numerical magnitude (across both formats) for each participant we calculated the lateral deviation difference between mirror-imaged displays (e.g., the lateral deviation difference between a participant's average trajectory when reaching toward a 1v2 display and their average trajectory when reaching toward a 2v1 display). We have previously shown that this analysis of trajectory differences between reaches toward mirror displays yields the most sensitive measure of a reach biases induced by the cue displays (Chapman et al., 2010a).

Our E1 analysis was designed to answer two main questions: (a) whether a given condition (combination of format and processing time) yielded a significant magnitude bias in reach trajectories and (b) what the relative effects of format and processing time would be. To address the first question, for each of the four conditions, we conducted a t test of lateral deviation difference at 100 ms against zero. A significant result indicates sensitivity to magnitude in that condition. To address the second question we conducted a 2 (Format: Dot versus Numeral) × 2 (Processing Time: Immediate versus Delay) mixed analysis of variance (ANOVA, repeated measures on format, between participants on processing time) on the lateral deviation differences (1v2 – 2v1 as described above) between trajectories at 100 ms. Repeated measures ANOVA results are reported with the Greenhouse-Geisser correction applied.

Experiment 1 results

The results for Experiment 1 are depicted in Figure 2 where we show the average reach trajectories generated by both the immediate (Figure 2a, b) and delay (Figure 2c, d) groups for both dot (Figure 2a, c) and numeral (Figure 2b, d) blocks. The results from the t tests assessing magnitude sensitivity can be seen visually in Figure 2e where the error bars represent the 95% confidence intervals for that difference relative to zero. As can be seen, for the immediate group (Figure 2e, left bars), only the dot difference (green bar) was significantly larger than zero, $t(19) = 2.88$, $p < 0.01$, whereas the numeral difference (gray bar) was not, $t(19) = 0.73$, $p > 0.47$. However, for the delay group (Figure 2e, right bars), both the dot, $t(18) = 5.38$, $p < 0.01$, and numeral differences, $t(18) = 4.85$, $p < 0.01$, were larger than zero. Thus, this analysis demonstrated that in the immediate condition only dots resulted in a bias of reaches to the side of space with the higher magnitude, whereas in the delay condition, the 500-ms preview was sufficient such that both dots and numerals resulted in a bias of reaches toward the higher magnitude.

The results from the mixed ANOVA revealed a marginally significant interaction between format and processing time, $F(1, 37) = 3.97$, $p = 0.054$. To further explore this, we conducted comparisons of dot and numeral performance across the immediate and delay groups. We found that the dot difference was not significant, $t(37) = 0.49$, $p > 0.6$, whereas the numeral difference was marginally significant, $t(37) = 2.14$, $p = 0.04$. The ANOVA interaction between format and processing time suggests that these two formats may not be influencing reach behavior identically. The second experiment in this study was specifically designed to further test for this intriguing possibility.

Experiment 2 methods

E2 implemented a protocol that was identical to that of E1-delay with the exception that we now explored

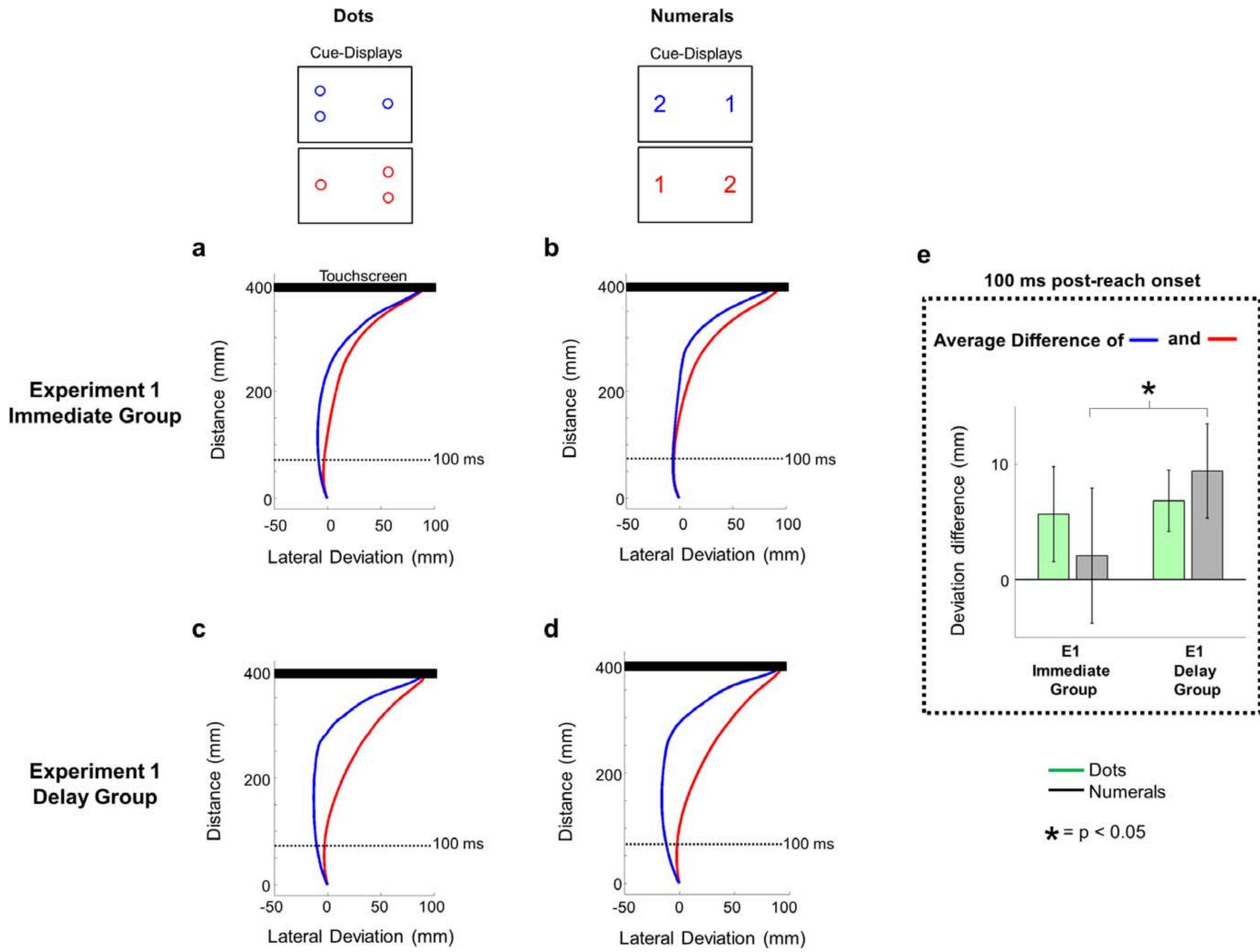

Figure 2. Results from E1. Mean reach trajectories for target ratios 2v1 (blue) and 1v2 (red) for both dot (a), (c) and numeral (b), (d) blocks in the immediate (a), (b) and delay (c), (d) groups. Results are shown for trials on which targets on the right were cued. The bars, shown in (e), denote the difference between the red and blue (red–blue) trajectory traces for dot (shown in green) and numeral (shown in black) blocks (i.e., the difference in lateral deviation between displays with more targets on the right and displays with more targets on the left) for trials on which targets on both the right and left were cued, plotted at a time point 100 ms post-reach onset (~70 mm of reach distance). Error bars show 95% confidence intervals and, when the lower boundary is greater than zero, they denote that differences diverged significantly ($p < 0.05$). Colors are for purposes of illustration only.

quantities within the small (1–3) and large (5–15) number range. Again, we ran two experimental groups: (a) a small-number group (E2-small) that encountered displays with values 1, 2, and 3; and (b) a large-number group (E2-large) that encountered displays with values 5, 10, and 15. To keep the number of different display types manageable, one side of the cue display always had a constant number of targets, either one target (on dot blocks) or the numeral 1 (on numeral blocks) for the small-number group or five targets or the numeral 5 for the large-number group. By keeping the number of targets on one side of the display constant, we were able to directly measure shifts in the incremental bias of initial reach trajectories as the number of targets increased from one (1) to two (2) to three (3) for the small number group and from five (5) to ten (10) to fifteen (15) for the large number group (for a similar parametric design, see Gallivan et al., 2011). To appreciate how the cue displays on numeral blocks and dot blocks compare, see Figure 3 (note that Figure 3 also denotes how on numeral blocks the numeral cue displays would have been subsequently replaced, at movement onset, with the corresponding dot display). Both the small-number group and the large-number group ran twelve 52-trial blocks (alternating between dots and numerals). The first block type was counter-balanced across participants, and the first block of each type was used as training and was not included in analysis (this yielded 260 analyzed dot and numeral trials each, see the Supplemental material for additional information regarding trial and participant screening).

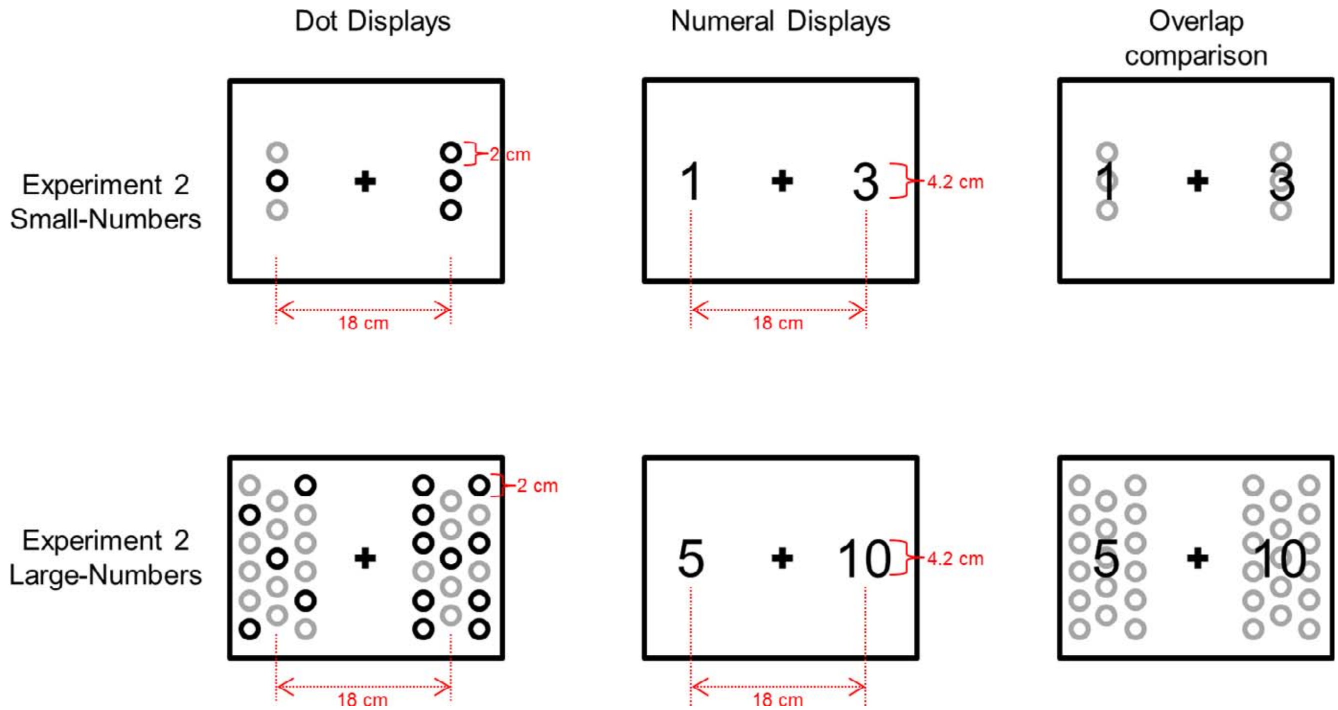

Figure 3. Parameters for dot and numeral cue displays in E2. Top row shows the cue-display parameters of a 1v3 trial for the dot display (left), numeral display (middle), and their overlap (right), for the sake of comparison. Bottom row shows the cue-display parameters of a 5v10 trial for the dot display (left), numeral display (middle), and their overlap (right). Gray outlined circles denote all possible target locations that could be displayed on a given trial whereas black outlined circles denote the potential targets for the example trial.

Experiment 2 analyses

We used the same dependent measure of reaching as described in the first experiment—that is, a measure of the lateral position of the hand 100 ms after reach onset. We again calculated biases induced by magnitude by taking the lateral differences between trajectories produced in different conditions. For this experiment we used an analysis that took advantage of our parametric design and calculated three key differences. Since we will include these differences as a factor in an analysis that can collapse across format, we will refer to them as ratio differences, which were preserved across number ranges. The first ratio difference is a single-unit increase in the quantity of the item opposite the constant value, comparing reaching toward 1v1 and 1v2 displays (small number group, where a single-unit increase of one occurs opposite the constant value) and 5v5 and 5v10 displays (large number group, where a single-unit increase of five occurs opposite the constant value). The second ratio difference is a double-unit increase in the quantity opposite the constant value, comparing reaching toward 1v1 displays and 1v3 displays (small number group, where a double-unit increase of two occurs opposite the constant value) and 5v5 and 5v15 displays (large number group, where a double-unit increase of 10 occurs opposite the constant value). Finally, the third ratio difference is again a single-unit increase in the quantity opposite the constant value, comparing reaching toward 1v2 and 1v3 displays (small number group, where a single-unit increase of one occurs opposite the constant value) and 5v10 and 5v15 displays (large number group, where a single-unit increase of five occurs opposite the constant value). To differentiate between the two single-unit ratio differences, we will refer to the first ratio difference (e.g., 1v1 to 1v2) as *single-unit low* and the third ratio difference (e.g., 1v2 to 1v3) as *single-unit high*. An analysis of these ratio differences allows an examination of how the trajectory bias changes across the three levels of magnitude increase. Importantly, we can then determine how these ratio differences compare in both the dot blocks and the numeral blocks and in the small and large number range (i.e., specifically testing for format and number-range effects in the trajectory data).

Similar to E1, our E2 analysis had two primary objectives: first, to determine whether a given condition (combination of format, ratio difference, and number range) yielded a significant magnitude bias in reach trajectories and second, to determine what the relative effects of format and ratio difference would be across both the small- and large-number groups. To address the first question, we again employed t tests of

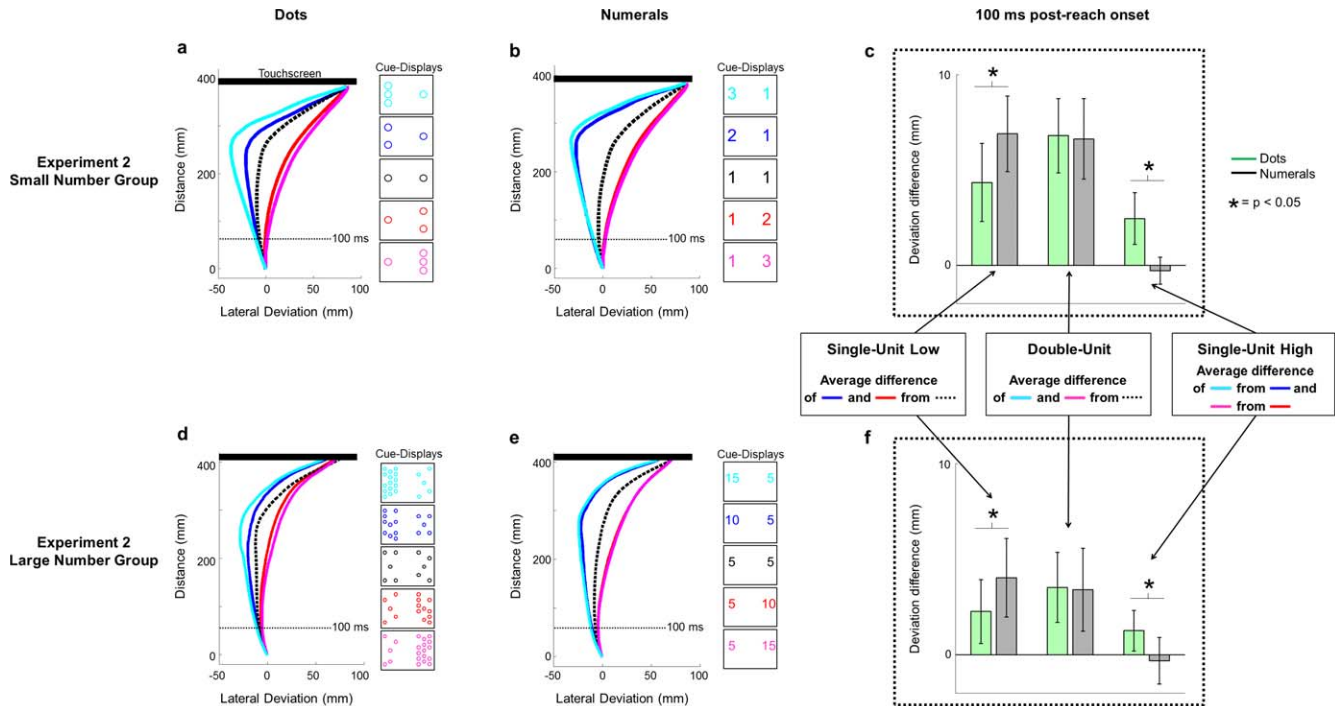

Figure 4. Results from E2. Results from the E2 small-number (a)–(c) and large-number (d)–(f) groups. The graphs in (a)–(b) show mean reach trajectories for target ratios 3v1, 2v1, 1v1, 1v2, and 1v3 for both dot (a) and numeral (b) experimental blocks. Results are shown for trials on which targets on the right were cued. (c) Left set of bars show the average difference between the single-unit-low trials for trials on which targets on both the right and left were cued, plotted at a time point 100 ms post-reach onset (~70 mm of reach distance); that is, red from black (red–black) and blue from black (blue–black) trajectory traces. Middle set of bars show the average difference between double-unit trials for trials on which targets on both the right and left were cued, plotted for the same time point; that is, the pink from black (pink–black) and cyan from black (cyan–black) trajectory traces. Right set of bars show the average difference between the single-unit-high trials for trials on which targets on both the right and left were cued, plotted for the same time point; that is, the pink from red (pink–red) and cyan from blue (cyan–blue) trajectory traces. Error bars show 95% confidence intervals and, when above zero, denote that differences significantly ($p < 0.05$) diverged. The graphs in (d)–(e) show mean reach trajectories for target ratios 15v5, 10v5, 5v5, 5v10, and 5v15 for both dot (d) and numeral (e) experimental blocks. Results are shown for trials on which targets on the right were cued. (f) Bar plots and associated confidence intervals are computed and shown the same as in (c). Colors are for purposes of illustration only.

lateral deviation difference at 100 ms against zero. To address the second question, we conducted a 2 (Number Range: Small or Large) × 2 (Format: Dot or Numeral) × 3 (Ratio Difference: Single-Unit Low, Double-Unit, Single-Unit High) mixed ANOVA (repeated measures on format and ratio difference, between participants on number range) on the lateral deviation difference at 100 ms.

Experiment 2 results

The results from E2 can be seen in Figure 4 where we show the average reach trajectories generated by both the small-number (Figure 4a, b) and large-number (Figure 4d, e) groups for both dot (Figure 4a, d) and numeral (Figure 4b, e) blocks. The results of the *t* tests examining magnitude sensitivity are again visualized using 95% confidence intervals of each difference relative to zero (see Figure 4c, f). For the small-number group, the single-unit low and double-unit ratio differences are significantly larger than zero for both the dot, single-unit low: $t(21) = 4.40$, $p < 0.01$, double-unit: $t(21) = 7.27$, $p < 0.01$, and numeral, single-unit low: $t(21) = 7.29$, $p < 0.01$; double-unit: $t(21) = 6.53$, $p < 0.01$, blocks. Importantly, however, for the small-number group and the single-unit high ratio difference, only the dot, $t(21) = 3.77$, $p < 0.01$, and not the numeral, $t(21) = 0.83$, $p > 0.42$, difference shows magnitude sensitivity. Strikingly, the identical pattern of results is seen for the large-number group. Again, the single-unit low and double-unit ratio differences are significantly larger than zero for both the dot, single-unit low: $t(16) = 2.88$, $p < 0.05$, double-unit: $t(16) = 4.06$, $p < 0.01$, and numeral, single-unit low: $t(16) = 4.15$, $p < 0.01$; double-unit: $t(16) = 3.26$, $p < 0.01$, blocks, while only the dot, $t(16) = 2.52$, $p < 0.05$, and not the numeral, $t(16) = 0.55$, $p > 0.58$, block shows sensitivity for the single-unit high comparison.

Together, these results indicate that when planning motor behavior, magnitude representation is format dependent in both the small and large number range. Specifically, in dot displays, as the number of items opposite a constant value increased from one to three for the small-number group (Figure 4a) and from five to 15 for the large-number group (Figure 4d), there was a graded increase in the initial trajectory bias toward that side of space (in accordance with the probabilistic distribution of targets). In the dot displays for example, not only was the initial trajectory more biased in the 2v1 and 10v5 conditions than the 1v1 and 5v5 conditions (single-unit low), it was also more biased in the 3v1 and 15v5 conditions than the 2v1 and 10v5 conditions (single-unit high). Strikingly, however, for numeral displays in both the small (Figure 4b) and large (Figure 4e) number groups, we found a "winner-take-all" response where the initial trajectories were biased by the same extent toward the larger numeral, regardless of the actual quantity it represented (i.e., whether it was a 2 or 3 or a 10 or 15, resulting in the null numeral bias we see in the single-unit high results).

The results of the mixed ANOVA confirm and extend these t test results. There are three significant results derived from this ANOVA and each is informative. First, we find a main effect between our two experimental groups, $F(1, 37) = 5.67$, $p < 0.05$. Here, the overall trajectory biases generated in the small-number range are larger than the biases generated in the large-number range. Given that this is the only significant effect involving number range (i.e., number range does not interact with format or pair difference) it could suggest that there is a specialized system for processing small numbers, regardless of their format. We explore this and other explanations in the discussion.

The second effect is a significant main effect of pair difference, $F(1.29, 47.59) = 40.34$, $p < 0.01$. Here, the results follow expectation, with the largest bias (5.17 mm) found for the pairs containing the largest differences (i.e., double unit) and a smaller bias found for the pairs containing the smallest difference (i.e., single-unit low: 4.40 mm, single-unit high: 0.78 mm, all Bonferroni corrected pairwise comparisons $p < 0.05$). In addition, we also see evidence, consistent with the Weber fraction, that equivalent magnitude differences are less salient at the higher end of a range of numbers. That is, there was a significant pair-wise difference in trajectory deviation between our single-unit low and single-unit high ratios (Bonferroni corrected $p < 0.05$). This means that the difference of one (opposite the constant value of one in the small number group) and the difference of five (opposite the constant value of five in the large number group) was more salient (leading to larger reach biases) when moving from one to two targets (i.e., 1v1 compared to 1v2, single-unit low) and from five to 10 targets (i.e., 5v5 compared to 5v10, single-unit low) than it was when moving from two to three targets (i.e., 1v2 compared to 1v3, single-unit high) or 10 to 15 targets (i.e., 5v10 compared to 5v15 single-unit high).

The third and most important effect is a significant interaction between format and pair-difference, $F(1.11, 41.17) = 14.16$, $p < 0.01$, indicating that the format of the numerical magnitude is having very different effects across both the small and large number range. Specifically, Bonferroni-corrected post-hoc tests show that for the single-unit-low pairs, the dot difference is significantly smaller than the numeral difference, $t(38) = 3.33$, $p < 0.01$. For the double-unit pairs, there is no difference between the dot and numeral difference, $t(38) = 0.037$, $p > 0.9$. Finally, for the single-unit high pairs the dot difference is significantly larger than the numeral difference, $t(38) = 4.23$, $p < 0.01$. This pattern is exactly what is predicted if the dot trajectory response is graded while the numeral response is winner take all. That is, as one moves from one set of dots to twice as many dots to three times as many dots opposite a constant value, we find a gradual increase in bias. However, as one moves from one numeral value to a numeral value with twice the magnitude to a numeral value with three times the magnitude opposite a constant value, we find strong biases to the larger numeral value, regardless of its magnitude.

General discussion

In this study we used a modified version of a recently developed rapid reaching task (see Chapman et al., 2010a, 2010b; Milne et al., 2013; Wood et al., 2011) to test whether the quantity information derived from different number formats (nonsymbolic dots versus symbolic Arabic numerals) would be used to guide the planning of motor movements in the same way. Across two experiments and four different experimental groups, we provide definitive evidence that the extraction of magnitude information for the purposes of behavior is highly format dependent. That is, the quantity information conveyed through dot and numeral displays biases planning-related processes in significantly different ways. In E1 we demonstrate format-dependent timing differences in the ability of individuals to use magnitude information, with dot information reliably being used immediately and with numeral information only reliably being used following a brief delay of 500 ms. Once these timing differences were accounted for in E2, we then found that format-dependent processing of quantity extended to both the

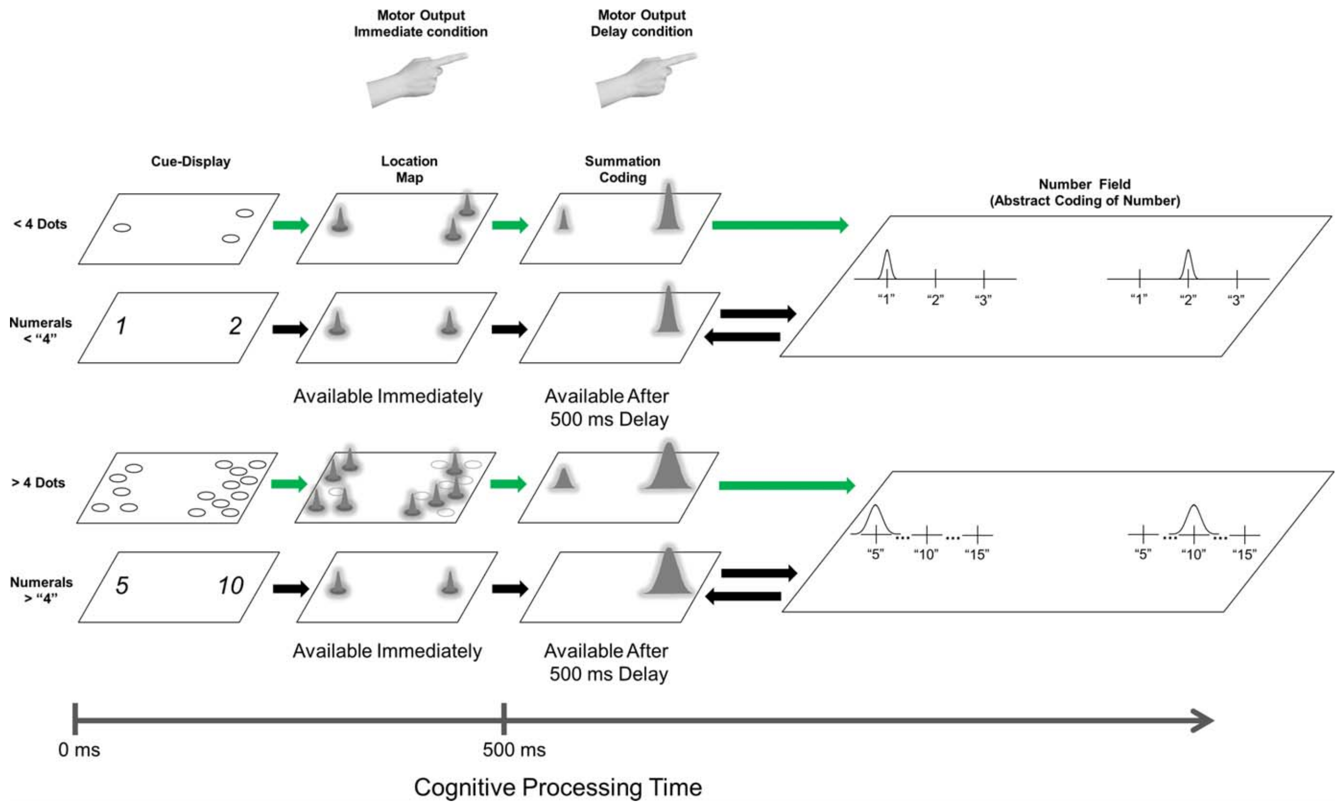

Figure 5. Hypothesized descriptive model explaining why the extraction of numerical quantity information differs between numerical formats and small and large number displays. See text for detailed descriptions.

small-number (e.g., 1–3) and large-number (e.g., 5–15) ranges. We also observed, quite unexpectedly, that individuals, as revealed through their initial reach trajectory biases, were more sensitive to changes in numerical quantity within small (1–3) than large (5–15) number ranges, regardless of their format. Here we discuss each of these key findings in light of how visual information about magnitude, derived from different formats, is used to guide the planning of actions at different exposure times. Then, after establishing this timeline, we attempt to consolidate our findings within the general framework of a descriptive model (depicted in Figure 5).

Initial effects of visual onset of the cue display (0-ms delay)

The first major finding of the present study, revealed in E1, is that only nonsymbolic (dot) information is immediately available to the visuomotor system (as evidenced by biases in the initial reach trajectories, see Figure 2). This was not an entirely unexpected result, given that previous researchers in the field have argued that different numerical formats—regardless of their eventual encoding (abstract vs. nonabstract)—necessitate different amounts of initial processing time (see Cohen Kadosh & Walsh, 2009). What we believe is more important, however, is that the immediate availability of nonsymbolic magnitude information is restricted to items within the small number range. In a previous study we showed, using a task that directly matches the timing of the E1-immediate condition, that reach trajectories were increasingly biased toward the side of the display containing more dot targets up to a limit of about four (see Gallivan et al., 2011). Any dot increases beyond this range, however, resulted in no additional increases in the trajectory bias. This was the case even when we increased the number of dots contained on one side of the display up to eight (in one experiment) and even 16 (in a second experiment). In light of the current and previous findings, the first aim of our descriptive model (expanded upon further below) will be to account for why small nonsymbolic magnitudes are immediately available to the systems involved in action planning in a way that larger nonsymbolic magnitudes simply are not.

Effects of additional cue-display processing time (500-ms delay)

A second major finding of the present study, revealed in E2, is that magnitude information derived both from large numbers of nonsymbolic dots and from symbolic numerals also becomes available to the visuomotor system following additional cue-display processing time (as evidence by biases in initial reach trajectories, see Figure 4). However, as comparisons between the two groups of E2 show, exactly how this information is used to plan movement fundamentally differs depending of the numerical format of the display (dots vs. numerals). Specifically, we found that reaching toward displays with dots resulted in incremental increases in the trajectory bias towards the side of the display with more dots. For example, in the group of participants exposed to small numbers (1–3), as the number of dots on one side of the screen (opposite a constant target with a value of 1) increased from one to two to three, the trajectory was biased less toward one, more toward two, and the most toward three. In striking contrast, reaching toward displays with numerals resulted in a winner-take-all trajectory bias. That is, as the numeral value opposite the constant target increased from 1 to 2 to 3 there was a large increase in trajectory bias from 1 to 2 but no additional increase as the numeral value increased from 2 to 3. Perhaps most importantly, in the second group of participants in Experiment 2, we show that the identical pattern of results holds for larger numbers with the exact same target ratios. That is, we show a graded increase in reach trajectory bias (albeit less than that found for the corresponding small number displays, as discussed further below) as the number of dots is increased from five to 10 to 15 and a winner-take-all trajectory bias when the same magnitude is conveyed by the numerals 5, 10, and 15.

Taken together, these 0-ms and 500-ms results require our descriptive model to account for two important features of the data. First, with reference to our previous work that reported a capacity limit of approximately four dot targets (Gallivan et al., 2011, see our discussion above), why is the magnitude information extracted from a large number of dots (five or higher) only available after a 500-ms delay while the magnitude information extracted from a small number of dots (four or less) is available immediately? Second, how does the extraction of magnitude information from nonsymbolic dot displays differ from that of symbolic numeral displays, leading to the numerical format differences observed across both the small and large number ranges?

A last major finding of the present study, also revealed in E2, is that the biases in reaching induced by small magnitude displays (1–3) were significantly larger than the biases induced by large magnitude displays (5–15), irrespective of both the number format (dots vs. numerals) and the fact that the same target ratios were controlled across both experimental groups (this effect was manifest as a significant group difference). We suspect that this small-number magnitude sensitivity, although quite unexpected for the symbols displays, may be tightly linked to the dedicated mechanisms thought to underlie the parallel individuation of small nonsymbolic numerosities, as described above (for example, see also Kaufman et al., 1949; Luck & Vogel, 1997; Pylyshyn & Storm, 1988; Revkin et al., 2008, for other similar small-set size effects). To the extent that smaller numerals (1, 2, and 3) had a greater influence on initial reach trajectories than their larger numeral counterparts (5, 10, and 15), this suggests that the representation of small numerals must be influenced by or perhaps rely upon the mechanisms supporting parallel individuation (a notion that has generated a great deal of debate, for reviews, see Le Corre & Carey, 2007; Piazza, 2010). Note, however, as detailed in the descriptive model below, that for this to be true, numerals and nonsymbolic dots need not share a common route to effecting action (indeed, our data strongly suggests the contrary, given that we found substantial differences depending on number format in the small number range). Rather, we only intend to suggest that perhaps through excessive exposure, learning, and rehearsal, small-number numerals may take on some of the specialized characteristics of the specific set sizes they represent (we expand upon this notion further below).

Descriptive model of numerical magnitude extraction

Motivation for the model

Before delving into the key theoretical details of our descriptive model, we first consider why a rapid motor task appears particularly well suited to identifying the format- and magnitude-dependent nature of numerical processing. When vision is used to guide real-time behavior it is thought to selectively extract those visual features linked to the real-world physical properties of objects (size, shape, density, etc.) in the environment (Goodale & Milner, 1992). In this way, the quantity information conveyed by a collection of discrete items (e.g., dots) can be thought of as an immediate visual property of that collection (in fact, visual features other than quantity have been shown to also influence magnitude estimates, Gebuis & Reynvoet, 2012). By contrast, the magnitude information conveyed by a single numerical symbol is cognitively removed from the visual immediacy of an actual set of items. That is, a numeral is a single visual item that, although representative of a particular magnitude, cannot be deconstructed into the visual/physical properties of the magnitude it represents (e.g., the numeral 3 bears no visual relation to its physical counterpart, three individual items). Thus, at the level of object feature processing for action, it seems rather intuitive that a visuomotor task be used to investigate numerical format differences.

Providing a first proof-of-principle for this idea, we have shown elsewhere (Gallivan et al., 2011) that the immediate extraction of quantity information from nonsymbolic displays is intimately tied to the well-documented basic visual capacity of object enumeration or *parallel individuation* (i.e., up to ~ four items), a bottleneck often linked to our ability to distribute attention to multiple locations across space (Bays & Husain, 2008; Hyde & Spelke, 2011). The real-world observation that spatial attention appears closely coupled to overt action processes (e.g., eye movements, reaches, grasps, etc.) has prompted several theoretical frameworks to unite spatial attention and movement planning processes in the explanation of goal-directed motor behavior (Baldauf & Deubel, 2010; Bisley & Goldberg, 2010; Cisek & Kalaska, 2010; Moore, Armstrong, & Fallah, 2003; Rizzolatti, Riggio, Dascola, & Umilta, 1987). Several variants of this general framework argue that behaviorally relevant objects in our environment compete in parallel for action selection, forming complex *attentional landscapes* or *salience maps* with hills of neural activity forming at the locations of these objects in space (Bisley & Goldberg, 2010; Fecteau & Munoz, 2006; Gottlieb, 2002; Gottlieb, Kusunoki, & Goldberg, 1998). Perhaps not coincidentally, the types of location maps proposed by theories of nonsymbolic magnitude processing and implemented by the neuronal models (Dehaene & Changeux, 1993; Verguts & Fias, 2004) look like and function very similarly to the location maps denoting objects of behavioral relevance, as used by the theoretical frameworks that unite spatial attention and movement planning processes. Taken together, it seems quite likely that this basic parallel individuation system, and by extension the numerical processing of nonsymbolic items, may be evolutionarily rooted in the more primitive mechanisms that support rapid reflexive motor planning and behavior (see also Dehaene & Changeux, 1993, for a similar suggestion). This notion is in line with the basic capacities of nonsymbolic numerical processing (i.e., up to ~ four items) observed in semifree-ranging monkeys (Hauser, Carey, & Hauser, 2000) and preverbal infants (Feigenson et al., 2004), who both lack symbol manipulation capabilities. In contrast, it is clear that symbolic number processing and manipulation requires far more advanced cognitive mechanisms (e.g., additional top-down connections) allowing the formation of more abstract associations (via prefrontal cortex, see Nieder, 2009; Nieder & Dehaene, 2009) and perhaps also the development (or evolution) of distinct brain areas in the human visual system (Shum et al., 2013), both of which are not likely to fall within the evolutionary purview of early visuomotor structures.

Explanation of the model

Building on this understanding of the potential links between parallel individuation and the location maps thought to underlie the encoding of behaviorally relevant objects and basic enumeration capacities, we now turn to the specific details of our descriptive model. This model extends the framework and employs the terminologies put forward in two predominant neural models of number encoding (Dehaene & Changeux, 1993; Verguts & Fias, 2004) and, as suggested above, is intended to unify models using location maps as a precursor for basic enumeration and as an index of behaviorally relevant objects. We accomplish the latter by proposing here that there is only one location map and it serves both purposes (action planning and object enumeration). It is worth noting that this model seeks only to extend these previous frameworks so as to account for the empirical data we present here and have found previously (Gallivan et al., 2011). As such, it does not, of course, capture the true complexity of visual processing, but might help in clarifying our theoretical understanding of magnitude processing and its link to motor control.

Recall that the results of our study demand that at least four questions be addressed by our descriptive model:

1. Why is the quantity information contained in small-number nonsymbolic cue displays available immediately to guide action?
2. Why is more processing time required to extract large-number nonsymbolic magnitudes?
3. Why is more processing time required to extract numeral magnitudes (regardless of number range)?
4. Why do we observe a larger reach bias generated by small numbers as compared to large numbers, regardless of their format?

To answer these questions and consolidate our understanding of the purpose of a location map, we propose that visual stimuli in most circumstances are represented in at least three distinct, temporally separated, stages: (a) as they are processed in space, (b) as their magnitude/quantity is extracted, and (c) as they are semantically linked to an abstract quantity. We refer to these three stages as a location map, summation code, and abstract number field, respectively, in order to most closely align descriptions of our model with previous terminology put forward by others (Dehaene & Changeux, 1993; Verguts & Fias, 2004). We link our model to behavioral output (in this case, reaching trajectories) by proposing that motor processes read out the quantity information from either the location map or summation codes in accordance with how long the visual information has been available for processing: Under limited time constraints (such as the 0-ms delay in E1-immediate group), information represented in the location map is exclusively used to guide reaching; under more relaxed time constraints (such as the 500-ms delay in E1-delay and E2 groups), reaching can now be influenced by information represented at the summation coding stage. Critically, given evidence from the current study indicating that motor planning processes do not reflect an abstract (i.e., format independent) representation of numerical quantity, our model assumes that the content of the abstract number field is never used as a basis for generating behavior.

Why is the quantity information contained in small-number nonsymbolic cue displays available immediately to guide action?

It has been reliably shown from neurophysiological recordings across a wide variety of brain areas that, upon the presentation of multiple visual stimuli in the environment, objects are transiently processed in parallel and compete for selection before additional top-down mechanisms select one of them for action (for reviews, see Cisek, 2007; Cisek & Kalaska, 2010). This parallel coding of objects rapidly gives rise to a location map with hills of neural activity at the spatial position of each object in the visual scene (Fecteau & Munoz, 2006; Gottlieb, 2002). However, this parallel individuation of objects, as noted above, has a limited resource capacity, simultaneously processing only about four objects in parallel. As shown in the location maps in Figure 5, when the number of objects on one side of space is greater than four, only four of those individual objects (on each side of space) can be processed in parallel. Thus, even though the actual display might have more dots on one side of the display than another (e.g., five vs. 10), the comparison at the level of the location map is roughly equivalent (~four vs. four). Likewise, because the numeral cue displays only ever contained two separable symbol items on the screen (one on each side of space), the comparison at the level of the transient location map is again roughly equivalent (~one item vs. one item), regardless of the actual quantities that those numerals denote. Consequently, based on the features of this descriptive model, when participants are forced to reach towards cue displays with very little processing time, their reach plans are informed only by the current information contained in the transient location map. As such, both large-number dot displays and numeral displays would be predicted to show no net trajectory bias toward the side of the cue display with the higher magnitude, which is exactly what we observe. In contrast, with a small-number dot display (less than four items on each side), each dot competes equally for processing resources in the location map and thus accounts for the observed trajectory biases toward the side of space with more targets.

Why is more processing time required to extract large-number nonsymbolic magnitudes?

Here we briefly turn to previous neuronal models of both magnitude encoding and decision making that formalize how, when given enough time, signals conveying magnitude information can arise. In numerical processing models, following the transient coding of items in a location map, this information is then summed across the map and stored in what is referred to as a *summation code*. These summation codes are still broadly spatially based (as in the location map) but importantly now reflect aggregated magnitude information (i.e., a rough count of the number of objects present, see Dehaene & Changeux, 1993). This summation process is very similar in principle to the integrative processes thought to underlie decision making when individuals are presented with two or more competing options to be acted upon (for reviews, see Cisek & Kalaska, 2010; Gold & Shadlen, 2007). In decision-making models, the options being considered (which often include decisions between multiple target locations for eye movements or reaches) require time for sensory evidence to be accumulated in favor of one action versus another. Only after enough time has elapsed such that one option reaches a sufficient threshold or *decision boundary* is there a resultant behavioral output indicative of the decision (Gold & Shadlen, 2007). Regardless of the particular type of model employed, the general finding is that, given time, these later stages of processing (e.g., a summation code) can begin to reflect features of the stimulus that are cognitively removed from those simple first visual features specifically tied to the objects in space (e.g., those contained in the location map).With respect to the dot cue displays in the current study, we suspect that additional processing time allows either for more complex visual features to be used in estimating numerical magnitude (e.g., density, a property requiring the integration of objects over space) or, alternatively, for the summation process to be fully completed across all items in the display. This, we believe, explains why large numbers of dots only begin affecting reach trajectories following a brief delay period (e.g., 500 ms).

It is also worth noting that, in general, the finding that it takes longer to initiate responses with more options accords with Hick's Law (whereby simple choice reaction time scales with the number of choices available, see Hick, 1952). However, our results differ from a classical Hick's finding in two ways: First, our results do not manifest in reaction times (see Supplemental material for full analysis) but rather in reach trajectory. We believe this is because we enforce such a rigid and rapid reaction time deadline (325 ms). Thus, participants generate rapid responses, and the type of processing delays that you would usually expect to find in reaction times are pushed into the movement phase, manifesting as the trajectory deviations we observe. Second, it is not clear if Hick's law applies to the rapid enumeration of small sets of items, or subitizing—the process that we believe guides the small-dot rapid reach behavior. In general, reaction times for enumerating small set sizes are fast and accurate for one to about four objects (Kaufman et al., 1949; Trick & Pylyshyn, 1994). Beyond four, however, reaction times for enumeration do scale with set size, getting longer with more options. It could be that this scaling in the large number range in part relies on the same kinds of mechanisms that lead to Hick's law.

Why is more processing time, regardless of number range, required to extract numeral magnitudes?

With respect to the numeral cue displays in the current study, we suspect that additional processing time (e.g., 500-ms delay) allows for a different process to occur than that noted above; specifically, it allows for a learned magnitude association, stored in an abstract number field, to be accessed and then, based on the features of our model, returned to the level of the summation code. In the abstract number field (and related representational spaces), the representations of numerosity are divorced from any analog measure of magnitude, and as such, it is likely that they are coded only relatively (see Lyons, Ansari, & Beilock, 2012, for a similar arugment). That is, while in the abstract number field a magnitude relationship (e.g., greater than) can be established, this is independent from and not likely accompanied by any precise notion of the degree of difference. It may be this highly abstract, more relational nature of numeral encoding that gives rise to the winner-take-all trajectory biases we observe. In contrast, as described above, since the magnitudes of nonsymbolic dot displays are derived from an actual physical stimulus dimension that can vary in an analog fashion (conveyed in both the location map and summation code), the differences between increasing magnitudes are necessarily graded (as observed in the incremental biasing of reach trajectories). (It is critical to note that it is the graded sensitivity we observe for all dot displays as opposed to winner-take-all motor responses for all numeral displays that gives us confidence that reach trajectories are not generated from the abstract number field.)

Why do small numbers, regardless of format, generate larger trajectory biases than large numbers?

At first glance, this finding might appear at odds with our general result that numerical format has profound effects on reach planning. However, upon closer examination, we believe it is the discrepancy between where motor processes access magnitude information versus where abstract magnitude information is stored in our model that accounts for this highly novel and important finding. As indicated above, our model proposes that motor actions can access magnitude information either very early in processing from the location map (~0 ms delay) or later in processing from the summation code (~ 500 ms delay), but importantly *not* from the abstract number field (indeed, if this were the case then we should find no differences between the number formats as they would both converge upon and be read out from a common representation). We do recognize, however, that an abstract number field (or some similar type of representational space) must exist for a numerical symbol, through either development or learning, to become associated/linked with a particular magnitude value derived from real physical properties (indeed, the abstract number field provides an important basis for neuronal models of symbolic processing, see Verguts & Fias, 2004), with the magnitude information from nonsymbolic stimuli (contained in the summation code) eventually converging onto some type of abstract number representation. When viewed from this perspective, it would not be particularly surprising then that small-number numerals should inherit at least some of the specialized characteristics (e.g., high precision) of the dedicated mechanisms that support the individuation of their small-number nonsymbolic counterparts, as shown here. Indeed, others have even suggested that symbols are initially grounded only within the subitizing range and then become abstracted to encompass larger quantities (Le Corre & Carey, 2007). Concerning debates as to whether number symbols acquire meaning by being mapped onto quantity representations supporting the approximate number system (Gallistel & Gelman, 1992; Piazza et al., 2007; Verguts & Fias, 2004), thought to support the representation of all quantities with a precision governed by Weber's law, or the parallel individuation system, already well described above (Carey, 2001, 2009; Piazza, 2010), the interpretation of our behavioral findings above would suggest that both systems are utilized by number symbols (see also Feigenson et al., 2004; Le Corre & Carey, 2007; Spelke & Kinzler, 2007). Another possibility, however, is that the range effects observed here for number symbols, rather than being derived from the nonsymbolic parallel individuation system, instead reflect the much higher frequency with which small number numerals are experienced. The relatively low frequency with which individuals interact with symbols of high numerical magnitude is a cross-cultural and cross-linguistic phenomena (Dehaene & Mehler, 1992) and it is possible that dedicated (and more precise) neural mechanisms are developed, through both learning and experience, for dealing with more frequently encountered symbols and/or stimuli (e.g., Kobatake, Wang, & Tanaka, 1998; Rainer & Miller, 2000). Thus, it remains a possibility that the effect of number range across the two formats may be underpinned by different processes—in the case of nonsymbolic quantity it is parallel individuation and in the case of symbolic quantity it is cultural and linguistic frequency. In any case, given that the effect of number range was a between-subjects factor in our study, we are cautious in making any strong claims concerning the findings and future investigations will be required to disentangle the intriguing possibilities noted above.

Again, it is worth emphasizing that unlike symbolic numeral information which, in order to be accessed by the motor system, likely must be fed back onto the corresponding summation code (or similar type representational spaces), magnitude information derived from dots can be accessed directly from the summation code itself. We believe that it is the combination of the dedicated mechanisms supporting small-number processing (either from parallel individuation or cultural/linguistic frequency) plus the indirect way in which numeral information must be accessed by the motor system that accounts for why both format-dependent and magnitude-dependent effects can coexist in our data.

Summary

There are vibrant and ongoing debates concerning the extent to which numerical processing in the brain (a) is format dependent versus independent (e.g., reviewed in Cohen Kadosh & Walsh, 2009) and (b) relies on a single shared estimation system versus an additional separate dedicated system for small set sizes (e.g., reviewed in Piazza, 2010). These debates largely rest upon discrepancies found in a wide variety of visual–perceptual tasks in which human participants either consciously count, compare, track or recall the numerical magnitudes presented. Here we took a rather distinct approach to addressing these questions and examined, using a rapid movement task, whether motor planning processes might reveal unique insights into how numerical quantities are processed and extracted for the guidance of visual–motor behavior. We found that reach planning was influenced in both a format-dependent and number range-dependent manner and, rather unexpectedly, that small-number stimuli, regardless of their format, were selectively processed. In addition to informing investigations and theoretical frameworks within the field of numerical cognition, these findings suggest that the use of a visuomotor task can provide substantive insights into the psychological mechanisms that support high-level cognitive capabilities in general and the representation of number in particular.

Keywords: number, symbolic, nonsymbolic, quantity, movement planning

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