Journal of Numerical Cognition
jnc.psychopen.eu | 2363-8761

PsychOpen publishing psychology

Research Reports

What Is in a Reach? Domain-General Spatial Modulation of Motor Responses by Number Representations

Santiago Alonso-Diaz*[a], Elon Gaffin-Cahn[b], Bradford Z. Mahon[acd], Jessica F. Cantlon[a]

[a] Department of Brain and Cognitive Sciences, University of Rochester, Rochester, NY, USA. **[b]** Department of Psychology, New York University, New York, NY, USA. **[c]** Department of Neurosurgery, University of Rochester Medical School, Rochester, NY, USA. **[d]** Center for Visual Science, University of Rochester, Rochester, NY, USA.

Abstract

Gaze, pointing, and reaching movements are thought to provide a window to internal cognitive states. In the case of numerical cognition, it has been found that the left-right deviation of a reaching movement is modulated by the relative magnitude of values in a number comparison task. Some have argued that these patterns directly reflect the representation of a logarithmically compressed mental number line (direct mapping view). However, other studies suggest that the modulation of motor outputs by numerical value could be a more general decision-making phenomenon (response competition view). Here we test the generality of interactions between the motor system and numerical processing by comparing subjects' reach trajectories during two different nonverbal tasks: numerosity comparison and facial expression comparison. We found that reaching patterns were practically identical in both tasks – reach trajectories were equally sensitive to stimulus similarity in the numerical and face comparisons. The data provide strong support for the response competition view that motor outputs are modulated by domain-general decision processes, and reflect generic decision confidence or accumulation of evidence related to mental comparison.

Keywords: numerosity comparison, emotion comparison, motor planning, reach

Journal of Numerical Cognition, 2017, Vol. 3(2), 212–229, doi:10.5964/jnc.v3i2.28

Received: 2016-03-08. Accepted: 2016-09-14. Published (VoR): 2017-12-22.

Handling Editors: Silke Goebel, University of York, York, United Kingdom; André Knops, Humboldt-Universität Berlin, Berlin, Germany; Hans-Christoph Nuerk, Universität Tübingen, Tübingen, Germany

*Corresponding author at: 430 Elmwood Avenue, Rochester, NY, 14620, USA. E-mail: sadiaz@bcs.rochester.edu

When asked to point to the larger of two numbers, one presented to the left and another to the right, subjects trajectories take a medial route when the numerical distance is close, and a more direct one when it is far (Santens, Goossens, & Verguts, 2011; Song & Nakayama, 2008). Such results imply that motor computations are penetrated by cognitive processing – the task of comparing numbers interacts with the path of the motor response. Modulations of motor responses by cognitive processes are not exclusive to number but are observed across a variety of domains, including intertemporal discounting, random dot motion, and phonology (Chapman et al., 2010a; Dshemuchadse, Scherbaum, & Goschke, 2013; Freeman & Ambady, 2011; Freeman, Ambady, Rule, & Johnson, 2008; Friedman, Brown, & Finkbeiner, 2013; Gallivan et al., 2011; Koop & Johnson, 2013; McKinstry, Dale, & Spivey, 2008; Spivey, Grosjean, & Knoblich, 2005; van der Wel, Sebanz, & Knoblich, 2014).

Although prior research suggests that reach trajectories are affected by cognitive processes across a variety of domains, a strong test of the domain-generality of these effects would be to compare performance with stimuli from different domains within a common task. Such a test is important for determining whether number-based modulations of motor responses are domain-specific (Chapman et al., 2014; Dotan & Dehaene, 2013; Song & Nakayama, 2008) or domain-general (Alonso-Diaz, Cantlon, & Piantadosi, 2015; Santens et al., 2011). Surprisingly, to date, no studies have pitted domains against each other in equivalent reaching tasks to assess the effect of domain on dynamic motor behavior. In the literature on number processing, interactions between stimulus values and motor responses have only been tested with numerical stimuli alone (Chapman et al., 2014; Dotan & Dehaene, 2013; Gallivan et al., 2011; Milne et al., 2013; Santens et al., 2011; Song & Nakayama, 2008), and only one study tested a non-numerical condition but that study did not examine the generality of their effects (Dotan & Dehaene, 2013).

There are two hypotheses about how number representations relate to reach trajectories: 1) direct mapping, and 2) response competition (Santens et al., 2011). In direct mapping, number representations are projected onto the spatial layout of reach. Number representations are organized along a mental number line wherein small and large numbers are placed to the left and right side of space, respectively (Dehaene, Bossini, & Giraux, 1993; de Hevia & Spelke, 2009; Rugani, Vallortigara, Priftis, & Regolin, 2015; but see Núñez & Fias, 2015). Numerical positions in the spatial representation conform to a logarithmic scale: as numbers get larger their distances in the mental line get compressed (Dehaene, Izard, Spelke, & Pica, 2008; Nieder & Dehaene, 2009; but see Cantlon, Cordes, Libertus, & Brannon, 2009; Cicchini, Anobile, & Burr, 2014). Under this hypothesis, the mental number line, its left-to-right organization, and logarithmic scale directly maps to the spatial positions of reach trajectories – and some data support this hypothesis (Dotan & Dehaene, 2013; Song & Nakayama, 2008).

Previous studies using number stimuli in reach tasks have shown that reach follows a numerically-modulated spatial path resembling a logarithmically compressed mental number line (Dotan & Dehaene, 2013; Song & Nakayama, 2008). In one study (Dotan & Dehaene, 2013), participants saw a number, say 27, and had to locate it on a physical line bounded by two numbers (0 to the left, 40 to the right) by moving their index finger from a central starting position to the desired location. During a key portion of the reach (~450 ms to 700 ms) participants' trajectories reflected a logarithmic scaling of number. They also showed that during a control task in which participants moved their fingers to a position indicated with an arrow (no numbers involved) no logarithmic effects were found in reach trajectories. Based on those findings, the authors argued that the logarithmic scaling of subjects' reach trajectories in the numerical condition reflected computations unique to numerical representation.

In the response competition view, what influences reach is not the values of the numerical representations but how the response options compete during decision-making (Santens et al., 2011; Spivey et al., 2005). During decision-making, each response option accumulates evidence in its favor until one dominates (Spivey et al., 2005). Subjects' reach toward one choice option but their reach is pulled toward the alternative choice option depending on the relative strength of the evidence favoring each option. Accumulation of evidence is a domain-general feature of decision-making that describes a large array of behavioral and neural phenomena (Shadlen & Kiani, 2013), including numerical judgments (Dehaene, 2009). Under the 'response competition' hypothesis, reach trajectories are modulated by how decision-making evidence is accumulated in favor of the choice (Santens et al., 2011) or relatedly, how it is used to compute levels of confidence given the evidence (Alonso-

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Diaz et al., 2015). This view is not specific to numerical representation but applies broadly to any decision. Santens et al. (2011) advanced the argument that response competition explains numerical effects on reaching behavior by showing that numerically-modulated reach trajectories emerge regardless of whether the task requires left-to-right or right-to-left number mapping. In their study subjects responded left for numbers smaller than 5 and right for numbers larger than 5. They found that subjects' response trajectories were more medial for values numerically close to 5 than far from 5. However, when they reversed the mapping with small numbers requiring a right response and larger numbers a left response they found the same pattern. This shows that numerically-modulated motor responses are not a direct readout of a left-to-right oriented mental number line but instead could reflect something more general about reach trajectories during choice.

In brief, what distinguishes the direct mapping hypothesis from the response competition hypothesis is that 'direct mapping' is a domain-specific hypothesis about the underlying nature of number representations whereas 'response competition' is a domain-general hypothesis about decision-making.

We investigated reaching dynamics across domains by comparing behavior on a reach task with stimuli from two different categories: numbers and faces. The prediction under a 'direct mapping' of number to reach is that number stimuli will logarithmically modulate reach trajectories and facial stimuli will not. Faces do not have an inherently uni-dimensional spatial representation or logarithmic spatial scaling (Freeman et al., 2008). Thus, the prediction is that numerical value should modulate reach trajectories as a function of their ratio but ratio-based modulation should not be present when comparing faces as there is no evidence for direct mapping of facial attributes to logarithmic space.

Alternatively, under 'response competition' the similarity of the stimuli should modulate reach trajectories in comparable ways within both the face and number tasks (including the possibility of logarithmically scaled reach). Response competition affects decision-making similarly across all comparison tasks (Shadlen & Kiani, 2013). Thus, if reach traces reflect decision processes, they should correlate with the difficulty of the mental comparison within each domain. If the comparison is easy and both options are clearly discernable reach should be direct; if the comparison is hard and there is less confidence then reach should be relatively more medial because the other option exerts a pull on the response that is proportional to difficulty. This pattern of reach should occur both for faces and numbers.

Experiment: Number and Emotion Comparisons

Here we examined subjects' reach trajectories during mental comparisons of numerical values and facial expressions. Numerical and facial judgments provide a strong test of domain-general effects because they are known to engage distinct perceptual, cognitive, and neural circuits (Leopold, O’Toole, Vetter, & Blanz, 2001; McKone, Kanwisher, & Duchaine, 2007; Nieder & Dehaene, 2009; Said & Todorov, 2011).

Methods

Participants

22 participants were recruited for the number task (13 female; Age: *M* = 20.5 yrs, *SD* = 2.2 yrs) and 20 for the face task (9 male; Age: *M* = 19.8 yrs, *SD* = 2.62 yrs). All were right handed. Experimental procedures were approved by the Research Subjects Review Board at the University of Rochester.

Materials and Procedure

Number Task

Participants saw two arrays of dots, presented on the left and right side of a computer screen. After 200 ms, the arrays disappeared and subjects had to report with their index finger the stimulus that had more dots (Figure 1). Response trajectories were captured with a Northern Digital Optotrak 3020, sampling at 200 hz. The experimental procedure was implemented with the Psychophysics Toolbox in MATLAB (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997).

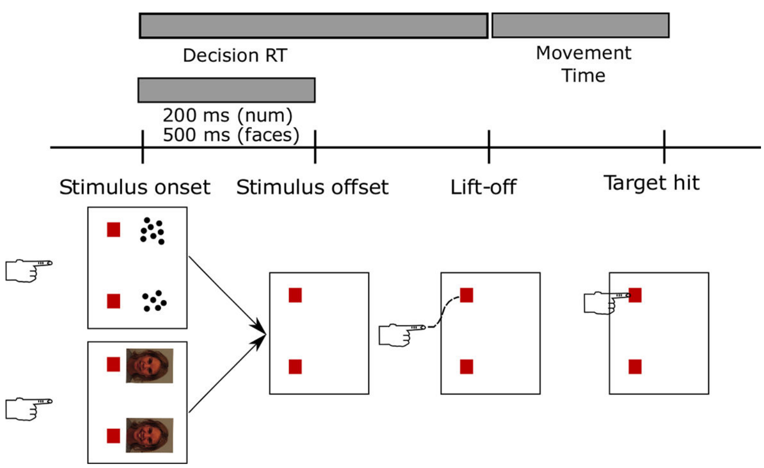

Figure 1. Number and face comparison task. Participants were asked either to report the larger number or the happier face.

Subjects sat approximately 55 cm from the screen (monitor information: 22" diagonal size, 1920x1080 resolution, 120 Hz). To initiate each trial, they had to hold a button with their right index finger, located 29 cm from the screen, centered along its midline (VPixx VP-BB-3 button box, dimensions of box: = 23 x 13 x 6 cm). Once the button was held for 1 s, two squares appeared—these two squares were the possible target landing spots for the reaching response. After 700 ms, the non-overlapping arrays of dots appeared on the screen for 200 ms, one to the left and the other to the right side of the screen's vertical midline. Participants were instructed to use their index finger to point to the target that had the greater number of dots. Movement sampling stopped when the index finger was 4 cm from the screen (this was a convenient distance used to avoid technical problems related to marker occlusion and signal fading). Feedback was not provided. Subjects were allowed to release the button and initiate the pointing response to one of the response squares at their own pace. The task consisted of 24 training trials and 420 test trials. Test trials were separated into 4 blocks, with 105 trials in each block. We presented numerical values in 5 numerical ratios (0.1, 0.25, 0.5, 0.75 and 0.9), with a maximum of 25 dots per array. Each ratio was shown 84 times. There were two trial types: 1) equal dot size for both sets (diameter: 40 pixels) and 2) equal cumulative area for both sets. Both types of trials appeared equally often. The order of the ratios and type of trial were randomized, as well as the side that had more dots (i.e., the response side). Dots were randomly configured within each array.

Face Task

The experimental procedure was identical to the number experiment but instead of arrays of dots, subjects saw two pictures of the same person with different expressions, ranging from neutral to happy (Figure 1 and 2). They were instructed to point to the happier face. Pictures were 281x381 pixels against a gray background. Stimuli were presented for 500ms. The 500ms exposure duration was determined based on a pilot study in which participants (n = 2) performed a response time (RT) version of the task (i.e. instead of reaching, responses were reported with the left and right button of a button box; 210 trials). One of these subjects was asked to prioritize accuracy over speed (RT: M = 749 ms, SD = 238, 93% correct), and the other to respond as fast as possible while trying to answer accurately (RT: M = 329 ms, SD = 57, 82% correct). The mean response time of both was 539ms, which we approximated to 500 ms. Faces were taken from the Karolinska Directed Emotional Faces database (KDEF) (Lundqvist, Flykt, & Öhman, 1998), validated in Goeleven et al. (2008). We used frontal angle pictures with happy and neutral expressions.

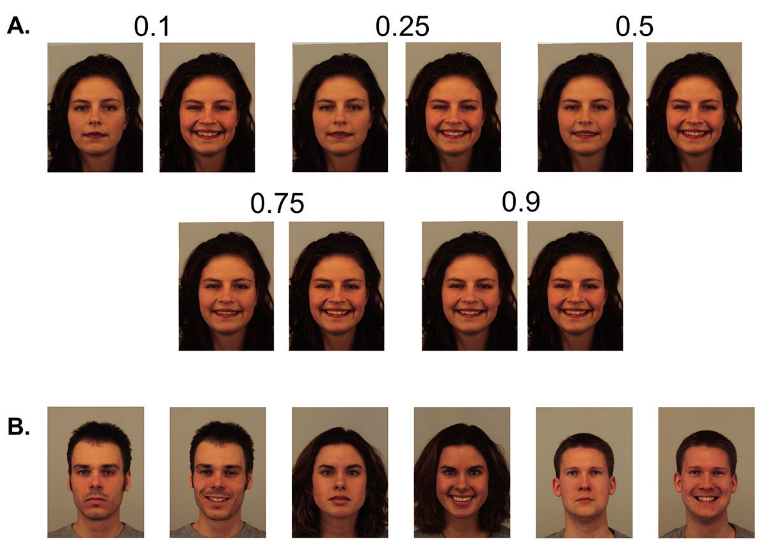

Figure 2. Example of face stimuli. A: An example of all the ratios presented for one of the faces. B: 3 samples of the 42 pairs used in the experiment.

To create a continuum of neutral to happy, we morphed the neutral expression with the happy expression in 100 steps. On any given trial, subjects saw a picture with the original happy expression and a morphed picture. Ratios were defined by the amount of morph-steps between the stimuli. For example, a 0.1 ratio trial was defined as a comparison between a neutral expression that was 10 steps into the morph versus the standard happy expression (Figure 2A). Morphing was carried out with the software Morph Age Express (Creaceed SPRL). We morphed 42 different face images, 21 males and 21 females. Each face had 5 ratios. The target face appeared equally often to the right and left side. This led to a total of 420 trials. The order of face presentation was randomized, with the constraint that the same face never appeared on consecutive trials.

Data Analysis

Response trajectories in which the subject pulled back or the marker was occluded were discarded (5.8% of trajectories). Of the remaining trajectories, only correct test trials were considered for all data analyses of reach and response times. Incorrect trials were few and mostly present in the hardest ratios (0.75 and 0.9). There was no additional information in these trials as response times and reach were slow and medial, as for correct trials. A correct trial was defined as a trajectory with 50% or more of points, including the end point, on the appropriate response side as defined by the midline of the screen (90% of trajectories). Considering only correct trials with this strict criterion is a conservative approach because any modulation is related to motor plans that were heading toward the target rather than the incorrect choice.

Trajectory coordinates were standardized to have 101 equally time-spaced points by means of linear interpolation (following standard practices in the literature e.g. Song & Nakayama, 2008; Spivey, Grosjean, & Knoblich, 2005). That is, each trajectory vector was resampled so that it had exactly 101 points (number of points in original trajectories: M = 127.01, SD = 50.13). We focused on the horizontal plane because the task options were arranged horizontally (Figure A1).

Stimulus similarity effects (based on numerical and face ratios) were tested with *functional ANOVAs* following Ramsay, Hooker, and Graves (2009). A functional ANOVA is a traditional ANOVA wherein effects of interest are computed at each time point of the interpolated reach trajectory (Ramsay et al., 2009). This analysis has been done before (Chapman et al., 2014; Gallivan et al., 2011; Milne et al., 2013), with the main advantage being that it tests effects across continuous dependent variables. We also performed traditional statistics on subjects' behavior for response time (RT), movement time, velocity, and mean horizontal positions. Response time was defined as the time between stimulus onset and lift-off, movement time as the time between lift-off and arrival to the screen, velocity as the mean magnitude of the velocity vector along the 3D trajectory, and mean horizontal positions as the average position on each trial along this axis.

All statistical tests and analysis were carried out with R (R Core Team, 2015).

Results

Discrete Measures

Overall, accuracy was equivalent in the number and face task (Average accuracy number = 90%; faces = 91%). An ANOVA with Task (number and faces) and Ratio (0.1 to 0.9) showed no main effect of Task ($F(1,40) = 2.01$, $p = 0.16$, $\eta_g^2 = .018$[i]), a main effect of Ratio ($F(4,160) = 491.91$, $p < .001$, $\eta_g^2 = .884$) and an interaction between Task and Ratio ($F(4,160) = 3.85$, $p = .005$, $\eta_g^2 = .056$). Figure 3 shows these results more clearly, revealing that accuracy was driven by ratio in both tasks and that the face task yielded slightly higher accuracy than the number task only on the most difficult ratios.

For response time (RT), there was a significant effect of Task ($F(1,40) = 22.07$, $p < .001$, $\eta_g^2 = .289$) and Ratio ($F(4,160) = 13.93$, $p < .001$, $\eta_g^2 = .065$). No effect of Side of Response ($F(1,40) = 0.17$, $p = .68$, $\eta_g^2 < .001$) nor any interaction (all p values > .4). Thus, subjects were overall faster with numerosities compared to faces (Figure 3) but the effect of ratio on RT was similar for both tasks.

Since RT is defined as the time between stimulus onset and liftoff, the slower RT for faces can be at least partly explained by differences in how the stimuli are encoded, taking less time for arrays of dots than facial expressions (Armann & Bülthoff, 2009; Cantlon & Brannon, 2006; Stoesz & Jakobson, 2013; Verguts, Fias, & Stevens, 2005; Walker-Smith, 1978). As for accuracy, the slight advantage for faces only on hard ratios may reflect slightly more precise mental representations of facial expressions compared to numerosities – again, an encoding effect.

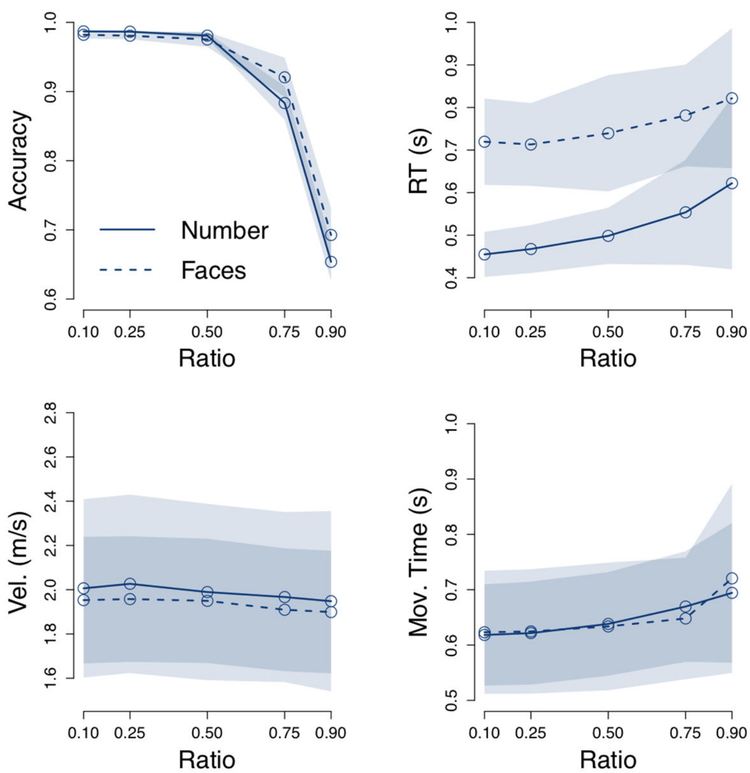

Figure 3. Performance and kinematics. Shading represents 2 s.e.m.

Discrete motor output was similar between the facial expression and numerosity tasks (Figure 3). An ANOVA of Task x Ratio x Side revealed that the velocity and movement time of subjects' reach trajectories were equivalent across tasks. For velocity and movement time, there were significant effects of Ratio (Velocity: $F(4,160) = 12.15$, $p < .001$, $\eta^2_g < .001$; Movement Time: $F(4,160) = 24.77$, $p < .001$, $\eta^2_g = .033$) and Side (Velocity: $F(1,40) = 43.17$, $p < .001$, $\eta^2_g = .002$; Movement Time: $F(1,40) = 164.58$, $p < .001$, $\eta^2_g = .029$). There was no effect of Task (Velocity: $F(1,40) = 0.29$, $p = .60$, $\eta^2_g < .001$; Movement Time: $F(1,40) = 0.01$, $p = .91$, $\eta^2_g = .030$) nor any interaction (all p values > .14). The similarity in discrete kinematic measures supports the response competition hypothesis that motor output should be similar across tasks.

We estimated Bayes factors for the ANOVAs with the BayesFactor package for R (Morey & Rouder, 2015), using 10,000 iterations. This test compares the probability of the data given two distinct hypotheses. It is based on the ratio of two marginalized likelihood models. If the value of the ratio is large it is interpreted as supporting the hypothesis of interest (further details in Gallistel, 2009; Jeffreys, 1961). We compared the null ANOVA (ratio, side, and interaction) against the task effect ANOVA (ratio, side, task, and interactions) for velocity and movement time. Both for velocity and movement time the Bayes factor favored the null model: 4381.14 ± 38%

and 209.53 ± 34%, respectively (as a rule of thumb, values greater than 3.2 are considered substantial, greater than 10 strong, and greater than 100 decisive in favor of the hypothesis of interest). This outcome supports the response competition hypothesis and indicates that during both face and number judgments, subjects approached the target with similar movement patterns (Figure 3).

Dynamic Analysis

The reach trajectories revealed clear ratio-based gradients during facial expression and numerosity judgments in the functional ANOVAs testing the effect of Ratio across the reach trajectories for each task (Figure 4). Figure 4 shows that for faces and numbers, stimuli elicited direct reach when the comparison was easy (e.g. 0.1 ratio) and closer to the midline when the comparison was difficult (e. g., 0.9 ratio). These results show that ratio modulated reach for both the face and number tasks, confirming the key prediction of the response competition hypothesis that stimulus difficulty modulates reach during mental comparisons.

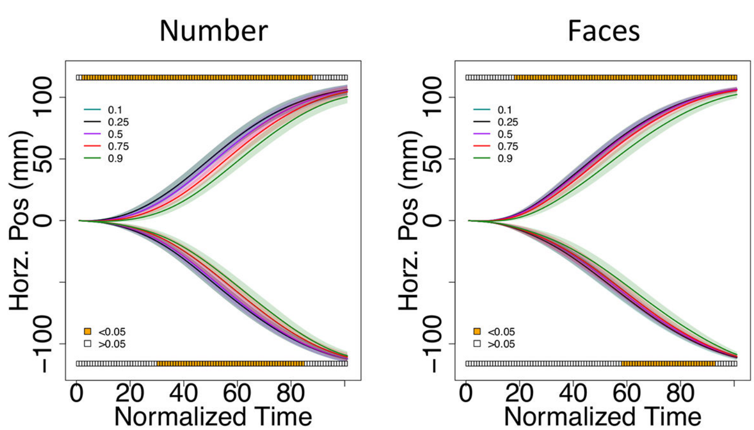

Figure 4. Reaching trajectories in the number and face task. Negative values are for the right side. The heat vectors above and below represent point wise significance levels for left and right ratio-dependent effects in reaching, respectively. Error shading is 2 s.e.m. As indicated by the effect of ratio on trajectory, both the number and face judgments elicited similarity-dependent spatial gradients in motor responses.

To characterize the pattern of spatial positioning we tested for compressive scaling in the modulation of reach trajectories by the stimuli. Compressive effects are known to emerge during numerical comparison (Nieder & Dehaene, 2009) but are not necessarily expected in the face domain. We explored these effects to see if we could detect any difference in the spatial layout of positions between numbers and faces. Specifically, at each point of time we modeled logarithmic patterns of positions by least-square fitting,

$$\text{Horiz. pos. (ratio)} = \text{Slope} \times \log(1\text{-ratio}) + \text{Baseline} \quad (1)$$

In Equation 1, slope is the rate of growth of logarithmic compression and baseline is an offset that determines how close horizontal positions are to the midline (e.g. if ratio = 0, then baseline is the maximal distance to the midline in trials with perfect information about numerical difference). An example application of this function to a reach trajectory is shown in Figure 5A. Interestingly, logarithmic compression successfully characterized the pattern of spatial positioning for both the numerosity and facial judgments (Figure 5B) (R^2 number task left: M = 0.97, SD = 0.02; right: M = 0.88, SD = 0.22; R^2 face task left: M = 0.90, SD = 0.14; right: M = 0.87, SD = 0.19). This result highlights the consistency across domains in how stimulus similarity affects motor output.

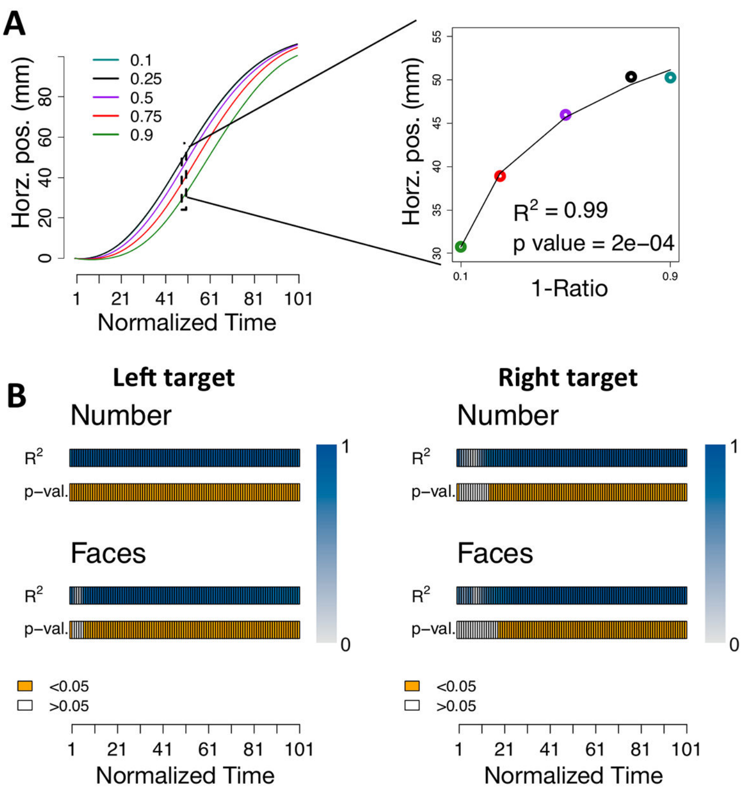

Figure 5. Spatial pattern of movement as a function of ratio along the average trajectory. A: Example of the fitting procedure for the left target in the number task. Right plot is a zoom of positions at the dashed rectangle (time slice 50). Circles are data and the solid line is the best-fit function. B: Main summary measures of the fitting procedure at each point of time for the left and right target. The heat bar at the right of each plot is for the R^2 measure of fit. Significance is colored with orange, non-significant with white.

Even though both tasks were well characterized by the same ratio-modulated reach pattern, the average slope of logarithmic positioning over time was larger in the number task than the face task. The baseline, which determines the maximal distance from midline at each point of time, did not differ between tasks. This was confirmed with unpaired t-tests comparing the average parameters from Equation 1 across time for each of the tasks (Figure 6A) (Slope L: $t(200) = 4.71$, $p < .001$, $d = 0.66$; R: $t(200) = -3.21$, $p = .002$, $d = 0.45$; Baseline L: $t(200) = -0.33$, $p = .740$, $d = 0.04$; R: $t(200) = -0.29$, $p = .774$, $d = 0.03$). The lack of difference in baseline shows that positioning is not significantly affected by an offset effect between tasks. The smaller slope for logarithmic effects in the face task versus the number task could, however, reflect non-compressive positioning for the face task (contra the prediction of the response competition hypothesis). We tested this possibility by comparing the logarithmic model with a linear model. This model comparison provides a statistical test of whether reach trajectories in the number and face tasks are explained by a common process. The logarithmic model was superior to the linear model for both tasks (Figure 6B) (Number: $t(402) = 4.78$, $p < .001$, $d = 0.47$; Faces: $t(402) = 9.25$, $p < .01$, $d = 0.92$; unpaired t-tests). The lack of task effects on patterns of reach is thus not serendipitous – the positive evidence of compressive positioning for both tasks reveals that reach trajectories are modulated by the difficulty of mental comparisons regardless of domain.

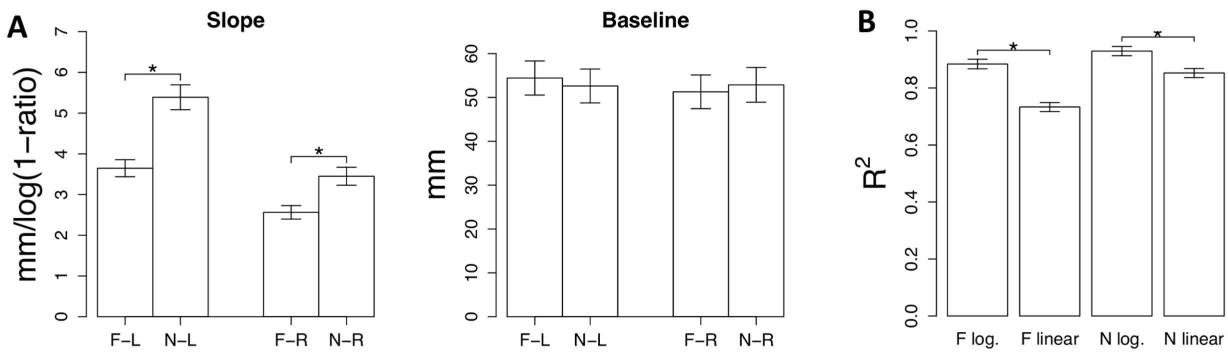

Figure 6. Average log. compression for each condition. A: Average slope and baseline for each task. Only slopes differed significantly, suggesting enhanced confidence in subjects that compared faces (see main text for details). B: Average logarithmic and linear fit across time (left and right side averaged). Compressive logarithmic positioning was better at explaining reach in both domains. F = faces task, N = number task, L = left target, and R = right target. Error bars are s.e.m.

*$p < .01$ (unpaired t-tests).

Slight differences in logarithmic slope between tasks can be explained by the fact that the number task had, on average, greater spread in the reach trajectories across ratios. A repeated measures ANOVA of Task x Ratio x Side over subjects' mean horizontal reach positions revealed an interaction between Task and Ratio ($F(4,160) = 4.19$, $p < .003$, $\eta_g^2 = .006$;) as well as a main effect of Ratio ($F(4,160) = 100.08$, $p < .001$, $\eta_g^2 = .124$). The main effects of Task ($F(1,40) = 0.72$, $p = .401$, $\eta_g^2 = .008$), Side ($F(1,40) = 3.47$, $p = .07$, $\eta_g^2 = .036$), and the remaining interactions were not significant (all p values for the interactions > .07). This indicates that trajectories were more extended in space across ratios during numerical judgments than facial judgments and this affected the slope. Because mean horizontal positions measure how attractive the other option was, the greater spread in the number task suggests that participants were overall more confident at lift-off during the face judgments compared to the number judgments. This interpretation also is consistent with the slightly higher accuracy reported for the face task. However, the important point is that the relative positions of the reach trajectories are both explained by a common compressive model in the face and number tasks (Figure 5 and 6B), showing a common underlying process.

One final observation about the logarithmic model is that it gave on average slightly better logarithmic fits to the left than to the right in the number task (R^2: L: $M = 0.97$; R: $M = 0.88$) but fit equally on both sides in the face task (R^2: L: $M = 0.90$; R: $M = 0.87$). A question that follows is whether this lateralization effect could be taken as evidence of a mental number line projected to reach. We do not think this is the case for two reasons. The first reason is that a better fit of logarithmic positioning only to the left side is not a prediction of the mental number line hypothesis. This hypothesis assumes a single scale going from left to right, equally logarithmically regardless of side. The second reason is that larger and smaller numbers appeared equally often on both sides – which means that the side differences in ratio scaling observed in our data are unrelated to number size (contra the direct mapping hypothesis). The effect of side on the fit of the logarithmic model to reach in the number task reflects a greater spatial spread across ratios on the left side, making the logarithmic pattern slightly more discernable with the R^2 measure. The cause of the greater spread on the left side during the number task is unclear but it is unlikely to be related to number line representation (Carey, Hargreaves, & Goodale, 1996; Chapman et al., 2010b; Gallivan et al., 2011).

Discussion

We found that motor output was similarly modulated by stimulus similarity during judgments in two distinct domains: numerical and facial processing. The speed, timing, and spatial pattern of subjects' motor responses were similar in almost every way during facial and numerical judgments. A Bayes factor analysis showed equivalent velocity and movement time patterns for the face and number tasks, reach trajectories in both tasks were significantly modulated by stimulus difficulty ratios, and a model comparison analysis over reach patterns showed that a compressive, logarithmic model best explains behavior for both tasks. Exceptions to the pattern of similarity included differences between the number and face tasks in the relative degree of compression between response sides and differences in the overall speed and accuracy of responding. However, we showed that the similarities between conditions far outweighed the differences and that the observed differences between conditions do not distinguish the direct mapping and response competition hypotheses. Overall, the data support the conclusion that a domain-general decision-making mechanism modulates communication between cognitive computations, such as numerical and emotional intensity, and motor planning processes. We now discuss the results in light of prior studies claiming domain-specific representations directly mapping to reach.

Direct Mapping View

In the number domain, the view that domain-specific representations can be captured with reach dynamics has been considered in at least three studies (Chapman et al., 2014; Dotan & Dehaene, 2013; Song & Nakayama, 2008). In the first study, and maybe the first attempt to connect reach and number representations, it was claimed that mental number lines could be detected within reach (Song & Nakayama, 2008). The critical result to support this view was obtained with an Arabic number-comparison task. In that task participants had to report whether a centrally presented number, say 3, was smaller, equal, or larger than a memorized standard, 5, by pointing to the left for smaller, center for equal, and right for larger. It was found that reach resembled a number line; for example, reach for number 1 was more to the left than reach for the number 2, 3, and 4 (and similarly with other numbers). The authors argued that a mental number line was projected to subjects' motor plans. It was later shown that the effect is symmetrical when reassigning the response codes as left larger, right smaller. In this reassigned response condition, reach for number 1 was further to the right than reach for number 2, 3, and 4, in clear contradiction with a domain-specific mental number line explanation (Santens et al., 2011). The alternative explanation of these effects is that they represent domain-general decision-making processes that use a generic distance metric. Our findings of comparable spatial and temporal patterns in reach behaviors during numerosity and facial judgments provide robust support for this domain-general view.

The second study arguing for a direct mapping of number to reach showed that reaching gestures reflect logarithmically compressed representations of numbers (Dotan & Dehaene, 2013). As described in the Introduction, the experimenters used a number-to-spatial position task. Participants saw a number and had to locate it on a physical line bounded by two numbers by moving their index finger from a central starting position to the desired location. Participants' reach trajectories reflected a logarithmic scaling of number but, during a control task in which participants moved their fingers to a position indicated with an arrow there were no logarithmic effects on reach trajectories (Dotan & Dehaene, 2013). Based on these findings, the authors argued that the logarithmic scaling of subjects' reach trajectories in the numerical condition reflected computations unique to numerical representation. However, the control task of arrow pointing did not involve mental comparison of stimulus values and thus it remained unclear whether logarithmic compression of reach trajectories are truly unique to numerical computations. Our results show that logarithmic effects in reach trajectories can be found during mental comparison tasks from non-numerical domain: face processing (also see Núñez, Doan, & Nikoulina, 2011). The logarithmic spatial patterns of reach trajectories likely have more to do with the relative difficulty of mental comparisons than with the specific scaling of numerical representations because similar patterns are observed across stimulus domains

A third study reported that reach was a window to symbolic and non-symbolic number formats (Chapman et al., 2014). In that study, participants had to hit a target that appeared on the left or right side of a screen monitor. The probability of the target appearing on each side of the screen was cued to the participants by numbers presented on each side before the target appeared. For example, if they saw the number 3 to the left and 5 to the right, it was more probable that the target would appear to the right[ii]. In one condition these numbers were Arabic numerals, and in another condition they were array of dots. The main result was that Arabic numerals always produced a decisive reach towards the side with larger target probability while the reach elicited by the array of dots scaled with numerical distance. Because of this difference it was claimed that number formats project to the motor system and influence reaching trajectories.

This interpretation hinged on the notion that reaching trajectories are modulated by number formats. However, the effect of format was weak because reaching trajectories were similar in symbolic and non-symbolic formats for low numbers and only differed at larger numbers (further details in Chapman et al., 2014). The authors argued that low number representations are similarly precise in symbolic and non-symbolic formats but high numbers differ in precision (Dehaene et al., 2008; Núñez et al., 2011). However, this interpretation of the effect is no longer about format but about difficulty and precision. That is, scaling in reach depends on how much confidence the numerical representation elicits, not what format it is in. This interpretation that scaling of reach reflects precision or difficulty is consistent with our findings as it can explain the modulation of reach by comparison difficulty in the number and face task.

Response Competition View

The results of the present study are most consistent with the response competition hypothesis (Santens et al., 2011; Spivey et al., 2005; Verguts et al., 2005). This framework proposes that response options compete during motor planning and exert a pull proportional to the evidence in favor of their respective response side. Variations of this idea have been used to explain many findings in numerical cognition (Faulkenberry, Cruise, Lavro, & Shaki, 2016; Faulkenberry, Montgomery, & Tennes, 2015; Marghetis, Núñez, & Bergen, 2014; Weaver & Arrington, 2013). These studies all describe phenomena related to response competition in numerical judgments. Our study shows that the influence of response competition on the spatial properties of motor behavior extends equally well to judgments of facial expressions and likely many other mental comparisons.

Recent research on the mental number line reported that logarithmic compression can be explained by adaptive decision-making (Cicchini et al., 2014). Cicchini et al. showed that each subject's spatial response during a number line task is predicted by that subject's previous exposures to numerical values, and greater logarithmic scaling (as opposed to linear scaling) is observed under high cognitive load than low cognitive load. Cicchini et al. showed that this pattern of responses is accounted for by a mathematical model of adaptive decision-making that weighs prior experience in future responding. Our results accord with those of Cicchini and colleagues (2014) and indicate that logarithmic effects in motor responses during numerical processing arise from decision-making processes.

Source of Difficulty-Modulation on Reach

An open question is whether reach modulation by degree of cognitive difficulty reflects pre-decision (encoding + pre-threshold accumulation of evidence) or post-decision processing (motor parameter settings + post-threshold accumulation of evidence) (see similar debate in Spivey, Dale, Knoblich, & Grosjean, 2010; van der Wel, Eder, Mitchel, Walsh, & Rosenbaum, 2009). Evidence that reach is modulated by difficulty even in self-paced paradigms (as the one used here) demonstrates that movement begins before cognitive processing is finished (Santens et al., 2011). This observation favors the pre-decision view because subjects spontaneously begin to reach but yet continue to show traces of cognitive processing in their movements – indicating that processing is still in a pre-decision stage at liftoff. However, we found that subjects' liftoff times also correlated with cognitive difficulty. This makes it hard to classify movement initiation and reach modulations purely as part of pre or post decision processing. Some have suggested using paradigms that force fast random movement initiation in order to definitively capture pre-decision processing in reach trajectories (Hehman, Stolier, & Freeman, 2015). However, this would not help explain our observation that reach modulations spontaneously emerge in self-paced paradigms after difficulty-dependent response times. Our results suggest a third possibility – that spontaneous choice reflects a single continuous processing stream in which encoding, mental comparison, decision, and response processes interact without discrete pre- and post-decision stages (Alonso-Diaz et al., 2015). This possibility is consistent with evidence that difficulty-modulated reach trajectories emerge across tasks, and regardless of whether subjects respond naturally or are forced to respond rapidly. It is also consistent with existing evidence that subjects are able to change their choice mid-reach (Resulaj, Kiani, Wolpert, & Shadlen, 2009). Direct comparisons of reach modulation during natural and rapid responses are needed to identify the root source of domain-general difficulty-modulated reach trajectories during mental comparison.

Conclusions

To answer the question of what is in a reach, we argue that motor plans inherit normalized information from domain-general mental comparison processes. This can explain the similarity of reach behaviors in the number and face tasks, and explain why trajectories are modulated by comparison difficulty across different cognitive domains. Reach patterns from mental comparison do not uniquely reveal a direct mapping of number to space but instead reveal how mental comparisons evolve in the mind.

A critical test for strong claims of domain-specific number effects in reach is to contrast results between numerical tasks and a comparable tasks in a non-numeric domain. This type of approach has been implemented to study the SNARC effect: the finding that in the Western educated mind low numbers are placed to the left and large numbers to the right (Dehaene et al., 1993). Early evidence suggested that the effect was specific to numerical processing, and did not generalize to alphabetic processing (Dehaene et al., 1993; though this is debated Chen & Verguts, 2010; Holmes & Lourenco, 2011; Rusconi, Kwan, Giordano, Umiltà, & Butterworth, 2006; van Dijck & Fias, 2011). A similar approach is useful for understanding the basis of other forms of numerically-modulated motor behavior. Our findings from spatially-modulated reach trajectories in numerical and facial processing highlight that some sources of number-space relations are domain-general interactions between decision-making processes and the motor system.

Notes

i) η_G^2 is the generalized eta squared, a measure of effect size. Criteria: .02 < η_G^2 < .13 small effect; .13 < η_G^2 < 0.26 medium effect; η_G^2 > .26 large effect (Bakeman, 2005).

ii) The probability was uniformly determined based on the numbers. In the example, the left side had 3/8 probability and the right 5/8 of probability. More details in Chapman et al., 2014.

Funding

Funding was provided by the James S. McDonnell Foundation (220020300) and the National Science Foundation (Education Core Research Grant DRL-1459625) to JC.

Competing Interests

The authors have declared that no competing interests exist.

Acknowledgments

The authors have no support to report.

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Appendix

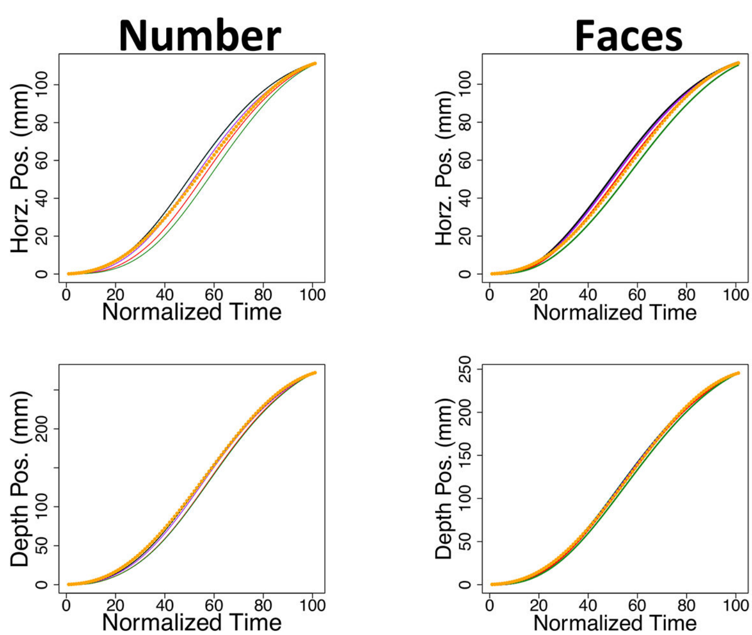

Figure A1. In both tasks, ratio effects were mostly noticeable in the horizontal coordinate (first row, color conventions for ratios as in main text). Also, reach was roughly optimal in the horizontal and depth axis i.e. the orange trace shows a trajectory that minimizes jerk (Flash & Hogan, 1985). This means that subjects were behaving as being biomechanically optimal, but interestingly mostly affected by ratio in their horizontal approach.

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