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Linear numerosity illusions in capuchin monkeys (*Sapajus apella*), rhesus macaques (*Macaca mulatta*), and humans (*Homo sapiens*)

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Abstract

Numerosity illusions emerge when the stimuli in one set are overestimated or underestimated relative to the number (or quantity) of stimuli in another set. In the case of multi-item arrays, individual items that form a better Gestalt are more readily grouped, leading to overestimation by human adults and children. As an example, the Solitaire illusion emerges when dots forming a central cluster (cross-pattern) are overestimated relative to the same number of dots on the periphery of the array. Although this illusion is robustly experienced by human adults, previous studies have produced weaker illusory results for young children, chimpanzees, rhesus macaques, capuchin monkeys, and guppies. In the current study, we presented nonhuman primates with other linear arrangements of stimuli from Frith and Frith's (1972) original paper with human participants that included the Solitaire illusion. In the current study, capuchin monkeys, rhesus macaques, and human adults learned to quantify black and white dots that were presented within intermingled arrays, responding on the basis of the more numerous dot color. Humans perceived the various illusions similar to the original findings of Frith and Frith (1972), validating the current comparative design; however, there was no evidence of illusory susceptibility in either species of monkey. These results are considered in light of illusion susceptibility among primates as well as the role of numerical discrimination abilities and perceptual processing mode on illusion emergence.

Keywords

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In many comparative studies of illusory phenomena, researchers focus on geometric illusions that emerge when a 2-dimensional object's size, length, color, or orientation is misperceived as a function of context. Numerous species have been the focus of studies on geometric illusions ranging from invertebrates (e.g., honeybees: Howard et al., 2017) to fish (e.g., Agrillo et al. 2013; sharks: Fuss and Schluessel 2017; redtail splitfins: Sovrano et al. 2015) to birds (e.g., pigeons: Fujita et al. 1991; Nakamura et al. 2008; grey parrots: Pepperberg 2017; chicks: Rosa Salva et al. 2013) to mammals (e.g., cats: Bravo et al. 1988; dolphins: Murayama et al. 2012; mice: Kanizsa et al. 1993). Of relevance to the current study, nonhuman primates perceive a variety of illusory phenomena consistent with human processing, including but not limited to the Ponzo illusion (Fujita 1996, 1997), the Müller-Lyer illusion (Suganuma et al. 2007), the horizontal-vertical illusion (Dominguez 1954), the Delboeuf illusion (Parrish and Beran, 2014; Parrish et al. 2015), the corridor illusion (Barbet and Fagot 2002), and the Zöllner illusion (Agrillo et al. 2014a), suggesting continuity in perceptual processing across the primates.

Another subset of visual illusions that are assessed in the comparative literature are numerosity illusions, in which the numerosity or quantity of stimuli comprising an array are mis-estimated based on spatial arrangement. These illusions are of particular importance as they shed light on the underlying numerical estimation abilities across species, as well as the potential similarities in quantity discrimination thresholds. As such, susceptibility to these illusions likely reflects a bias in the magnitude estimations of numerous species and may even explain species-level differences in quantitative acuity. For example, the regular-random numerosity illusion leads human adults and, under some circumstances, rhesus macaques to overestimate regularly arranged items relative to the same number of randomly arranged items (Beran 2006; Ginsburg 1976, 1980). In a similar illusion, the Solitaire array results in the mis-estimation of the relative quantity of items in an intermingled set. Frith and Frith (1972) first established the Solitaire illusion with human adults who were instructed to determine whether there were more black or white dots in an array comprised of 16 of each dot color equidistantly positioned in a cross pattern (Figure 1). This spatial arrangement leads to the over-estimation of the centrally clustered dot color relative to the dots located on the peripheries. Eight-year-old children also were tested, and they too were sensitive to the Solitaire illusion, but there were individual differences among the children tested. Frith and Frith (1972) discussed their results in light of Gestalt principles, with the items located on the periphery forming separate units whereas the centrally-clustered items formed a better Gestalt and thus appeared more numerous (Wertheimer 1923). Specifically, the laws of proximity and good continuation lead to grouping of elements close in space and that form a straight line. Thus, clustered or regular patterns evoke overestimates of numerosity whereas discontinuous or random patterns are relatively underestimated.

We extended the investigation of the Solitaire illusion to nonhuman primates, including chimpanzees (*Pan troglodytes*), rhesus macaques (*Macaca mulatta*), and capuchin monkeys (*Sapajus apella*) as these species have been used in a number of studies investigating geometric and numerosity illusions. All previous studies included a relative quantity discrimination task in which subjects were presented with multicolored arrays, such as black and white dots, and were required to select the set containing a greater number of dots of a

specific color. Control arrays with different numbers of dots of the two colors were presented for training and to verify that subjects were responding to the 'choose more' rule. When presented with the Solitaire illusion arrays, if subjects were sensitive to the illusion, they should have selected the set that contained the centrally-located dots of a given color. Chimpanzees were not sensitive to the Solitaire illusion even though they clearly were able to discriminate a variety of numerical ratios in control trials (Agrillo et al., 2014b). Rhesus monkeys and capuchin monkeys also performed well in control trials of previous studies but showed limited evidence of illusion perception, with variability among individual monkeys within both species (Agrillo et al., 2014b). In a subsequent study, we extended this task to human children (3 to 6 years of age) and task-naïve capuchin monkeys to isolate possible developmental and experiential influences in the emergence of this illusion (Parrish et al. 2016). Again, monkeys showed some evidence of illusion perception in this previous research but there were individual differences. There was an effect of age among children, with younger children performing more similarly to the monkeys (variable and overall weaker illusory experiences) and older children more consistently perceiving the Solitaire illusion similar to adults. This suggested a possible effect of human-unique experiences, or a developmental trajectory, giving rise to this particular illusion.

To determine the role of quantitative abilities on the perception of the Solitaire illusion, we also tested the limits of this illusion with human adults using a computerized quantity estimation task with speeded presentation to prevent counting (Agrillo et al. 2016b). During this previous study, adults were instructed to provide an estimate for the number of dots of one color that were presented in intermingled arrays. For example, if they saw a set containing 32 total dots with 12 white dots and 20 black dots, they should have reported the estimated number of white dots (12). For the Solitaire array, the dots located on the perimeter were perceived as being 76% as numerous as the centrally clustered dots (i.e., perimeter dots were underestimated in terms of numerosity relative to central dots). From a comparative standpoint, these results inform whether a given species may have the appropriate quantification abilities to perceive the Solitaire illusion. Furthermore, failure to perceive the Solitaire array may be a result of numerical sensitivity of a particular species or specific individual rather than the result of perceptual mechanisms (e.g., Gestalt grouping principles). In support of this, we recently documented perception of the Solitaire illusion among adult guppies (*Poecilia reticulata*) and found a correlation between illusion perception and numerical acuity in control trials (Miletto Petrazzini et al. 2018). There was increased sensitivity to the illusion among fish who had higher accuracy with the .78 ratio in control trials as well as among those fish who were faster at initially learning the numerical rule (Miletto Petrazzini et al. 2018), suggesting a link between numerical acuity and perception of this particular illusion.

In addition to the crossed-Solitaire pattern, Frith and Frith (1972) presented linear arrays of intermingled black and white dots to human participants. Dots of one color that formed a continuous line were found to be more numerous than dots of a different color that were spatially distant or formed an interrupted pattern (Figure 2). Similar to the cross-patterned Solitaire array, these linearly arranged dot illusions likely emerged due to the Gestalt principles of proximity and good continuation. To assess whether nonhuman primates are sensitive to the linear arrays from Frith and Frith's (1972) original study, we presented these

linear patterns to capuchin monkeys and rhesus macaques using a computerized relative quantity judgment task. We also tested a group of human adults to verify that the paradigm presented herein adapted for comparative work would elicit the illusion in humans.

Because of the variable nature of Solitaire illusion perception in past studies, we predicted individual differences may again emerge among capuchin monkeys and rhesus macaques when they were presented with the linear patterns. Although the linear patterns also may produce an overall weaker effect among monkeys akin to what was seen among human participants in Frith and Frith (1972), it is important to note that the present state of the literature on illusory experiences by nonhuman animals does not always align with reports from human participants. In fact, some failures to demonstrate illusions in animals challenge ideas about the phylogenetic emergence of certain mechanisms underlying these experiences for humans (e.g., Nieder 2002). For example, the evolutionary origin of low level non-cortical mechanisms underlying the perception of motion illusions (e.g., fixational eye movements, Gori et al., 2014) or brightness illusion (e.g., lateral inhibition in the retina, Agrillo et al., 2016a). Hence, quantitative illusions such as the Solitaire illusion and the linear illusions that seem to be related need to be assessed comparatively.

Experiment 1

Method

Participants—We tested 14 capuchin monkeys (8 females) aged 10 to 21 years and 7 male rhesus monkeys aged 15 to 35 years from Georgia State University's (GSU) Language Research Center (LRC). Capuchin monkeys were group housed in indoor/outdoor enclosures that included a variety of enrichment items. Rhesus monkeys were housed separately in indoor enclosures but had multiple weekly periods in which they were jointly housed with a preferred conspecific with access to outdoor enclosures that included a variety of enrichment items. All monkeys separated for testing sessions so that they had solo access to their computer station without competition from other monkeys. Capuchin monkeys had access to the computer apparatus for approximately 4-hour time blocks; rhesus monkeys had access to the computer apparatus for approximately 8-hour time blocks. Monkeys worked or rested as they chose. All monkeys received a daily diet of primate chow, fruits, and vegetables regardless of participation in the project. The calories consumed during the test session were factored into their diet to maintain a healthy weight as determined by veterinary staff. Test protocols and procedures were approved by the Institutional Animal Care and Use Committee of GSU (protocol numbers A16015 and A18047). GSU is accredited by the Association for Assessment and Accreditation of Laboratory Animal Care.

All monkeys had prior experience engaging with computerized testing, including tests of visual illusions and prior tests of the Solitaire array (Agrillo et al. 2014a, b; Beran 2006; Parrish et al. 2015, 2016).

Apparatus—Monkeys were tested using the LRC's Computerized Test System (Evans et al. 2008; Richardson et al. 1990), which included a color monitor, personal computer, digital joystick, and food pellet dispenser. Monkeys manipulated a joystick that controlled a cursor located on screen; the cursor could be directed to make contact with various stimuli

including the digital dot arrays presented in the present experiment. Monkeys viewed the monitor between 30.5 cm to 40.5 cm depending upon their position in the test enclosure. This was an uncontrolled aspect of the study because we do not restrain monkeys when they engage computerized tasks, and so there is variability in the distance from which they view the monitors. However, that is still within a range for which all species could see full arrays without any occlusion. Contacting the correct array led to delivery of a 45-mg banana-flavored pellet, whereas contacting the incorrect array led to a 20-s timeout period during which the screen remained blank. The program was written in Visual Basic 6.0.

Design and Procedure—All trials began with a light grey rectangular stimulus presented in the top middle of the computer screen, which had a dark grey background color. A cursor also appeared at the bottom middle of the screen, and the monkey began the trial by bringing the cursor into contact with that light grey rectangle. This occurred through manipulation of the joystick with the monkey's hand, which led to isomorphic movement of the cursor onscreen. Once selected, the light grey rectangle and the cursor disappeared, and the trial stimuli (linear dot arrangement) appeared on screen. On all trials, these stimuli consisted of circles (dots) that were 25 pixels wide and 22 pixels tall, presented at the top center of the screen. Each dot was presented somewhere in a grid that was three dots wide, and 12 dots tall. The inter-dot distance in both dimensions was 32 pixels from edge to edge of two adjacent dots. At the same time, a black rectangle appeared at bottom left of the screen, and a white rectangle appeared at the bottom right of the screen. These were the response icons, and monkeys chose one of those icons by moving a cursor centered between the icons into contact with one of them.

Each monkey began in the training phase, during which the task progressed through two steps. In the first step, a randomly determined number of dots from 3 to 6 was selected as the smaller set size, and the larger set was the resulting value of subtracting the smaller set from 24. One of these sets was randomly assigned as white dots, and the other as black dots so that sometimes there were more white dots and sometimes more black dots. There was equal likelihood of black or white dots as being the more numerous set and, subsequently, the correct response. Each dot then was randomly assigned a location within the 12×3 array of possible locations. Monkeys had to select the response icon that matched the color of the more numerous dot array intermixed at the top center of the screen. If the correct icon was selected, a melodic tone played, and the monkey received a single food reward. An incorrect response led to a buzz tone, and then a 20 s timeout period during which the screen was blank. When a monkey responded correctly in 42 trials or more of the most recent 50 trials completed, the next step was presented. In step 2, the smaller array size was randomly chosen from the range 4 to 11, and the larger set again was the result of subtracting the smaller array size from 24. When a monkey again met criterion of 42 of 50 trials correct, the test phase began.

In the test phase, each trial was either a baseline (non-illusory) trial or one of 12 possible illusory arrangements. We presented two versions of the six linear arrays from the Frith and Frith (1972) study, including the original six arrays in which the black dots created the better Gestalt (see Figure 2) as well as the inverse of these arrays in which the white dots created the better Gestalt. The probability of a given trial being a baseline trial was .85, and of being

a probe trial was .15. On baseline trials, the smaller set again was randomly determined from the range 4 to 11 items, and the larger set was the difference between that number and 24. Whether there were more black dots or more white dots on these trials was randomly determined. This allowed for a range of possible comparisons from very easy comparisons (e.g., 4 versus 20) to very difficult comparisons (11 versus 13). The top two panels of Figure 2 demonstrate the range of difficulty on baseline trials.

The illusory probe trials were of six possible arrangements, shown in Figure 2. Again, we presented each of these arrangements in the way shown in Figure 2, and also in version with the white and black dots reversed in position. This led to a total of 12 illusory arrays. In each of these arrangements, there were always 12 white and 12 black dots, and thus no correct answer. Based on Frith and Frith (1972), we divided the different illusory arrays into two categories: divided clusters (Figure 2, arrangements 1–3) and undivided clusters (Figure 2, arrangements 4–6). The former category is characterized by the fact that items forming two separate clusters (e.g., white dots) are presented at the two opposite sides of the group of dots forming a better Gestalt (black dots). The latter is defined by the presence of one dot on the same side ('undivided clusters'). Frith and Frith (1972) reported a stronger illusion in the presence of divided clusters.

On these illusory probe trials, monkeys were non-differentially reinforced for their choice, with a .50 probability of hearing the melodic tone and receiving a food reward for both choices, and a .50 probability of instead moving right to the next trial initiation stimulus for either choice. In this way, even though we used an operant conditioning procedure, monkeys could not learn how to respond to these arrays on the basis of differential reinforcement and punishment because there were no timeouts given for these probe trials and reward was non-differentially presented. Each monkey completed trials in the test phase to the point where 200 probe trials had been presented (with a similar number of presentations for the 12 illusory arrays), allowing a sufficient number of trials with each of the probe illusory arrangements to determine whether individual monkeys showed a bias to choose one set over the other.

Results

On average, capuchin monkeys needed 1,227 trials ($SD = 1,196$ trials) before reaching the learning criterion (see Table 1). Rhesus monkeys needed 1,236 trials ($SD = 1,885$; see Table 1). However, there was great variability in the number of training trials needed across individual monkeys. During the test phase baseline trials, a repeated measures ANOVA showed a main effect of the numerical ratio between sets of both species, meaning that accuracy of monkeys decreased linearly when the numerical ratio between the smaller and the larger quantity increased (rhesus monkeys Greenhouse-Geisser corrected, $F(3.511, 21.067) = 116.235$, $P < 0.001$, linear trend: $F(1, 6) = 519.040$, $P < 0.001$; capuchin monkeys: Greenhouse-Geisser corrected, $F(3.105, 40.366) = 187.829$, $P < 0.001$, Linear trend: $F(1,13) = 912.255$, $P < 0.001$; Figure 3). In particular, both species successfully discriminated even the hardest numerical ratio presented, 11 vs. 13 (ratio = 0.846): rhesus monkeys, proportion of accuracy: 0.633 ($SD = 0.045$), one sample $t(6) = 7.829$, $P < 0.001$; capuchin monkeys: 0.619 ($SD = 0.054$), one sample $t(13) = 8.150$, $P < 0.001$.

For illusory probe trials, we combined both versions of each illusory array, including the original six arrangements (Figure 2) and the inverse of those arrays with white and black dots transposed. We calculated the selection of the dot color forming the better Gestalt for the six illusory arrangements. Table 1 presents the results for each monkey with each stimulus arrangement for the probe trials. There was great variability among both species in the number of monkeys and the individual monkeys that showed a human-like illusory bias, or an opposite bias in some cases. When considering all 200 trials given to each monkey across all arrangements, two capuchin monkeys (Widget and Wren) out of 14 monkeys significantly selected the array forming the better Gestalt; one monkey selected the opposite pattern (Nkima; see Table 1). These data suggest that capuchin monkeys do not perceive numerosity illusions in the presence of these visual patterns.

At the group level for capuchin monkeys, no significant choice preference for either array was found in any arrangement [Bonferroni corrected alpha level of 0.01 to account for repeated tests; arrangement 1 ($t(13) = 1.390$, $P = 0.188$); arrangement 2 ($t(19) = 0.597$, $P = 0.561$); arrangement 3 ($t(13) = 0.673$, $P = 0.513$), arrangement 4 ($t(13) = 0.419$, $P = 0.682$); arrangement 5 ($t(13) = 0.899$, $P = 0.385$); arrangement 6 ($t(13) = -0.902$, $P = 0.383$)]. No significant difference was found when we compared the overall performance of monkeys in the presence of divided (Figure 2, arrangements 1–3) and undivided (Figure 2, arrangements 4–6) clusters (divided clusters, mean $\pm$ *SD*: 0.528 ± 0.084; undivided clusters: 0.505 ± 0.123; paired t-test, $t(13) = 0.719$, $P = 0.485$).

When considering all 200 trials given to each rhesus monkey across all arrangements, two monkeys out of seven (Han and Chewie) showed a bias to choose the array forming the better Gestalt (see Table 1). No rhesus monkeys showed the opposite bias. At the group level for rhesus monkeys, no significant choice for either array was found [Bonferroni corrected alpha level; arrangement 1 ($t(6) = 0.877$, $P = 0.409$), arrangement 2 ($t(6) = 0.703$, $P = 0.509$), arrangement 3 ($t(6) = 1.039$, $P = 0.339$), arrangement 4 ($t(6) = 2.017$, $P = 0.090$), arrangement 5 ($t(6) = 1.908$, $P = 0.105$) and arrangement 6 ($t(6) = 1.198$, $P = 0.276$), Figure 4]. No significant difference was found when we compared the overall performance of monkeys in the presence of divided (Figure 2, arrangements 1–3) and undivided (Figure 2, arrangements 4–6) clusters (divided clusters, mean $\pm$ *SD*: 0.536 ± 0.097; undivided clusters: 0.614 ± 0.113; paired t-test, $t(6) = -3.416$, $P = 0.014$).

To assess whether inter-individual differences could be related to differing numerical acuity of monkeys, we correlated the number of trials necessary to reach the criterion in the training phase with choices in the presence of the illusory patterns. No significant correlation was found (rhesus monkeys, $r = -0.194$, $P = 0.677$; capuchin monkeys, $r = -0.143$, $P = 0.625$). Similarly, no significant correlation was found when we assessed the accuracy in the most difficult ratio (0.846) with the overall performance in the presence of the illusory arrays (rhesus monkeys, $r = 0.061$, $P = 0.897$; capuchin monkeys, $r = 0.440$, $P = 0.115$).

Discussion

The majority of monkeys required fewer than 1,000 trials to reach criterion in the training phase. In this phase, monkeys were required to select the dot color that was more numerous in an array of randomly-arranged black and white dots. Monkeys learned to select either a

black or white rectangle that was associated with the larger number of dots in the intermingled set. Some monkeys from both species required 2,000 trials or more to reach criterion, but all subjects mastered this task.

The majority of monkeys of both species showed no bias on the linear arrangements, with equal likelihood of black or white responses in these illusory probe trials. There was very limited evidence of illusion susceptibility across species; two of 14 capuchin monkeys (Widget and Wren) significantly selected the array forming the better Gestalt and two of seven rhesus monkeys (Han and Chewie) significantly selected the array forming the better Gestalt. One of 14 capuchin monkeys (Nkima) perceived a reversed illusion opposite from humans (no rhesus monkeys showed the reversed bias). An important remaining question is how these data compare to data from adult humans, for whom this illusion was reported to be robust, but only in a single study. Thus, we gave this task to human adults for this comparative purpose.

Experiment 2

Method

Participants—Twenty adult human volunteers (14 females, 6 males) between the ages of 19 and 34 years (mean age 22.6 years) took part in the experiment. All had normal or corrected-to-normal vision. The task was approved by the ethics committee (Protocol 2576) of the Department of General Psychology of University of Padova (Italy). All participants gave their informed written consent prior to participating in the experiment.

Apparatus, Design and Procedure—For the human task, the procedure was similar to that described with monkeys, with a few exceptions. LCD color monitors (17 inches) and a cordless joystick (Logitech freedom 2.4) were used. No auditory feedback was given; no food reward was provided but rather participants saw visual feedback: The word "Correct" in green color or the word "Incorrect" in red color appeared within a rectangle placed in the middle of the screen. To avoid the use of verbal counting, participants had to respond within 2 seconds otherwise the trial was considered null. Timeouts for incorrect responses were shortened to only 8 s. As for the nonhuman primates, in illusory probe trials, there was non-differential reinforcement, with a 0.50 probability of positive feedback ("Correct") and a 0.50 probability of simply moving to the inter-trial interval.

Participants advanced from each training phase to test phase when they correctly completed 10 of the most recent 12 trials in which there was a real difference in the number of white and black dots. Each participant completed a total of 100 probe trials in a single session. Participants were instructed to select the color (black or white) associated with one of two groups of dots presented (both intermingled with black and white dots). Importantly, participants were not instructed to maximize or choose the color associated with the larger quantity.

In this way, we reduced the methodological variability between human and non-human primates as the rules for correct responding could only be inferred from the feedback, exactly as happened in the monkeys' experiment.

Results

On average, humans needed 22 trials ($SD = 4$) for reaching the learning criterion of the training phase (see Table 2). In illusory probe trials, humans were highly likely to show a response bias to some of these illusory arrangements but not others. This occurred for 18 of 20 participants for arrangement 1, for 19 of 20 for arrangement 2, for 12 of 20 participants with arrangement 3, for 5 of 20 participants for arrangement 4, for 7 of 20 participants for arrangement 5, and for 3 of 20 participants for arrangement 6. Only two human participants showed a reverse bias, and this was for arrangement 6.

At the group level, participants showed a bias for three arrangements (Bonferroni corrected alpha level, arrangement 1: $t(19) = 27.700$, $P < 0.001$; arrangement 2, $t(19) = 19.369$, $P < 0.001$; arrangement 3, $t(19) = 6.773$, $P < 0.001$). No significant bias was found for arrangement 4 ($t(19) = 2.860$, $P = 0.010$), arrangement 5 ($t(19) = 2.550$, $P = 0.020$) or arrangement 6 ($t(19) = 0.516$, $P = 0.612$; Figure 4).

A significant difference was found when we compared the overall performance of participants in the presence of divided (Figure 2, arrangements 1–3) and undivided (Figure 2, arrangements 4–6) clusters (divided clusters, mean $\pm$ SD: 0.893 ± 0.121; undivided clusters: 0.610 ± 0.169; paired t-test, $t(19) = 7.543$, $P < 0.001$). These results match closely those reported by Frith and Frith (1972).

Discussion

Human participants showed a clearer misperception of numerosity when tested in comparable conditions to those given to monkeys. Specifically, participants perceived the illusion for the 'divided clusters' but not for the 'undivided clusters', consistent with the original work. This indicated that stimuli and procedures adopted in Experiment 1 were appropriate to elicit the numerosity illusions studied in humans by Frith and Frith (1972). The different performances reported in rhesus and capuchin monkeys compared to humans are likely to reflect true differences in the sensitivity of numerosity illusions between these species.

General Discussion

We assessed susceptibility to the linear arrangements of the Solitaire array, first presented to humans by Frith and Frith (1972), and here presented to humans, rhesus monkeys, and capuchin monkeys. Under the current paradigm, human adults perceived the illusory arrays in a similar fashion to that reported in the original work, overestimating the number of dots in arrangements that formed a continuous line or that were spatially contiguous. It is interesting to note that the magnitude of the numerosity illusion seemed to depend on the degree of continuation between dots. The first three spatial arrangements (Figure 2, arrangements 1–3) produced a stronger numerosity illusion compared to the others. These patterns are characterized by the fact that items forming two separate clusters (white dots) are presented at the two opposite sides of the group of dots forming a better Gestalt (black dots). This condition was defined as 'divided clusters' by Frith and Frith (1972). In the current study, human adults did not misperceive the other three arrangements (Figure 2,

arrangements 4–6) that presented one color of dots on the same side ('undivided clusters'). Frith and Frith (1972) also reported a stronger illusion in the presence of divided clusters. Hence, our study replicated this result, reinforcing the idea that the emergence of a numerosity illusion is more robust for arrays whose elements form a better Gestalt.

Rhesus macaques and capuchin monkeys showed the well-established ratio effects in control trials, with higher performance for trials presenting larger numerical differences in dot colors and lower performance for trials presenting smaller numerical differences in dot colors. Ratio effects in quantity discrimination tasks have been replicated for these and other primate species in a variety of studies as well as a number of other animal species (see Beran et al. 2015; Brannon 2006 for reviews), suggesting an evolutionary-ancient and widespread ability to perceive and discriminate based on numerical information. Furthermore, both species were able to discriminate the hardest numerical ratio presented (0.85). This is an important finding as we have recently reported that items located on the periphery of the classic Solitaire array are perceived as 76% as numerous as centrally-clustered items by human adults (Agrillo et al. 2016b). Because monkeys in the present study were able to discriminate a more difficult ratio (0.85), we felt confident that they displayed adequate discriminatory abilities to potentially fall prey to these linearly-arranged numerosity illusions. However, there was only minimal evidence of sensitivity to the illusory dot arrangements.

When faced with a relative quantity discrimination task using only one dot color (versus intermingled sets as seen here), capuchin monkeys and rhesus macaques are sensitive to what is known as the density bias (Parrish et al., 2017). Although not ubiquitous to all monkeys, individuals of both species display a preference for sets containing densely-arranged items to sparsely-arranged items of equal quantity. Thus, capuchin and rhesus monkeys are sensitive to the overall density within arrays, but the relative density of intermingled items did not have the same overall effect on these animals as observed in the current study. A similar phenomenon concerning clustering has been documented recently among domestic chicks. When faced with two arrays of equal numerosity, chicks preferred higher clustering (perceived greater numerosity, akin to the density bias) but human adults preferred lower clustering (perceived greater numerosity; Bertamini et al., 2018). The authors discussed their results in light of the occupancy model in which surface area is positively correlated with perceived numerosity (Allik and Tuulmets, 1991). Individual elements within an array influence one another such that elements close in proximity are perceived as less numerous than those further apart, at least for human adults (for opposite results and evidence of the density bias among infants, see Uller et al., 2013). However, this leaves open the question of why monkeys would be sensitive to the density bias but not the Solitaire illusion? It may be that the density bias emerges for two discrete sets of stimuli that are compared without need to individuate specific elements in the arrays, whereas the Solitaire arrangements require such individuation (e.g., extraction of black dots from white dots). More work is needed to better assess this possibility and to consider the mechanism(s) responsible for this difference. These could include attentional processes, for example, or perhaps individuation draws upon resources that prevent or interfere with the misperception of quantity due to other grouping mechanisms.

It is worth noting that our previous work on the Solitaire illusion presenting the classic cross-patterned array (Figure 1) also included the majority of monkeys in the current study (Agrillo et al. 2014b; Parrish et al. 2016). Although the linear arrays presented in the current work are unique relative to the Solitaire arrangement, it is possible that previous exposure to the classic Solitaire array and other numerosity illusions may have weakened their susceptibility to the present stimuli. Future work is needed to test this hypothesis using task-naïve animals. Interestingly, there is not a consistent pattern of illusory perception across these studies, with little overlap in the emergence of the classic Solitaire pattern and the linear arrays presented herein. There were a number of monkeys that perceived the classic Solitaire illusion in these previous studies that showed no evidence of the illusion with the current linear arrays, although this is somewhat expected based on Frith and Frith's (1972) human work. Overall, perception of the Solitaire array, including the classic cross-patterned array (Figure 1) and the linear arrays (Figure 2), by both rhesus macaques and capuchin monkeys is weak and inconsistent relative to the pattern of results documented in human adults and older children (Agrillo et al. 2014, 2016b; Frith and Frith 1972; Parrish et al. 2016). Also, unlike with guppies (Miletto Petrazzini et al. 2018), there was no correlation between sensitivity to the illusion and performance in the control trials, suggesting that, unlike fish, the different sensitivity to this illusion in monkeys is not related to precision of quantity discrimination more generally.

We also found evidence of inter-individual variability for each spatial arrangement among humans. This is particularly clear in the presence of the 'undivided clusters.' However, even with spatial arrangements that elicited a strong illusion ('divided clusters'), there were human participants who were not sensitive to it. This result aligns with the inter-individual variability with the Solitaire illusion found by Frith and Frith (1972) and by Agrillo et al. (2016b) and, more generally, with the evidence that, although many illusory phenomena are perceived by most participants, there is often a proportion of individuals who are not sensitive to them (see Billino et al. 2009; Doherty et al. 2010; Fraser and Wilcox 1979). More work remains to be done regarding the source of individual variability in numerosity illusion sensitivity among human adults.

In the case of these illusions (both the classic Solitaire array and linear arrangements), items forming a better Gestalt through good continuation and proximity tend to be overestimated relative to the same number of items spatially separated. As capuchin monkeys and rhesus macaques appear to be less susceptible to such illusions compared to humans, the possibility exists that rhesus and capuchins' perceptual processing mode weakens their susceptibility to the current illusions as they demonstrate a local precedence, perceiving the local elements of a multi-item array prior to the overall, global configuration (*Macaca mulatta*: Hopkins and Washburn 2002; *Sapajus apella*: De Lillo et al. 2005, Spinozzi et al. 2003, 2009). Experimental work has shown that a species' local precedence can be shifted towards a human-like global precedence if items are positioned closer together and that capuchins are sensitive to item density in a variety of quantity discrimination tasks (De Lillo et al. 2005; Parrish et al. 2017; Spinozzi et al. 2003). Future work that varies the inter-item distance of the different-colored dots within these kinds of arrays (as opposed to simple manipulations of item arrangement) may provide support for the role of grouping principles in numerosity illusions.

Acknowledgments

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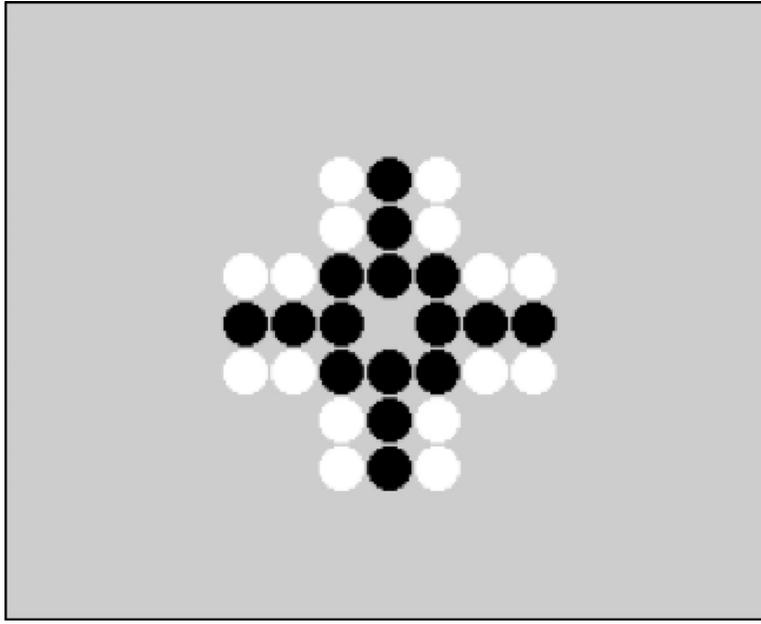
Figure 1.
The cross-patterned Solitaire array contains 32 dots, including 16 black and 16 white dots. Typically, the centrally-located black dots are over-estimated relative to the same number of white dots located on the periphery.
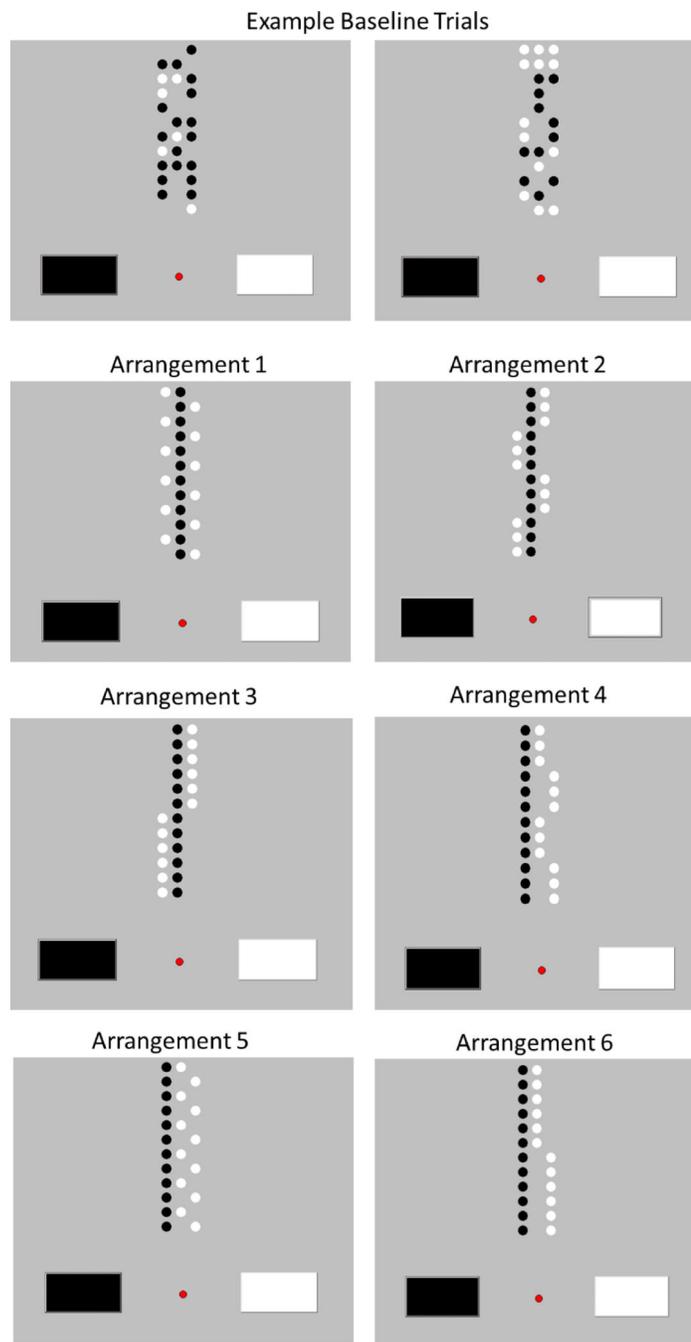
Figure 2.
Trial types presented in the experiments. The two top panels show a fairly easy (left) and hard (right) baseline trial type. In these trials, there was a difference in the number of black and white dots. The bottom six panels show the six illusory arrangements. For all illusory arrangements, the black dot is predicted to be perceived as more numerous. Arrangements 1–3 are the 'divided clusters' and arrangements 4–6 are the 'undivided clusters.
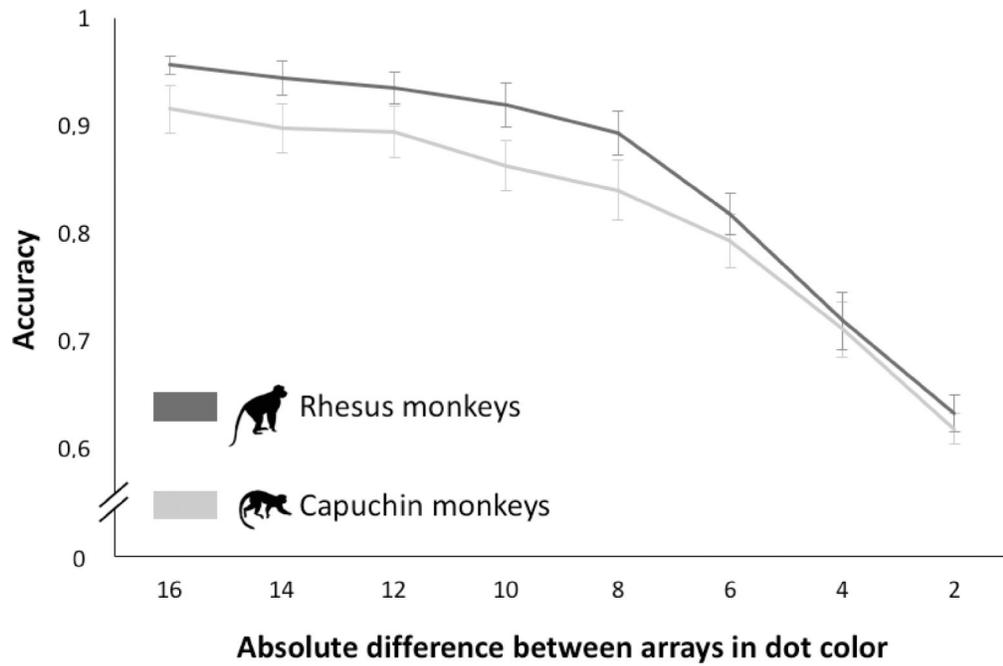
Figure 3.
Mean performance as a function of the difference between colored dots (black and white) within each array in test phase of Experiment 1. Smaller differences indicate objectively more difficult trials. Error bars indicate the standard errors.
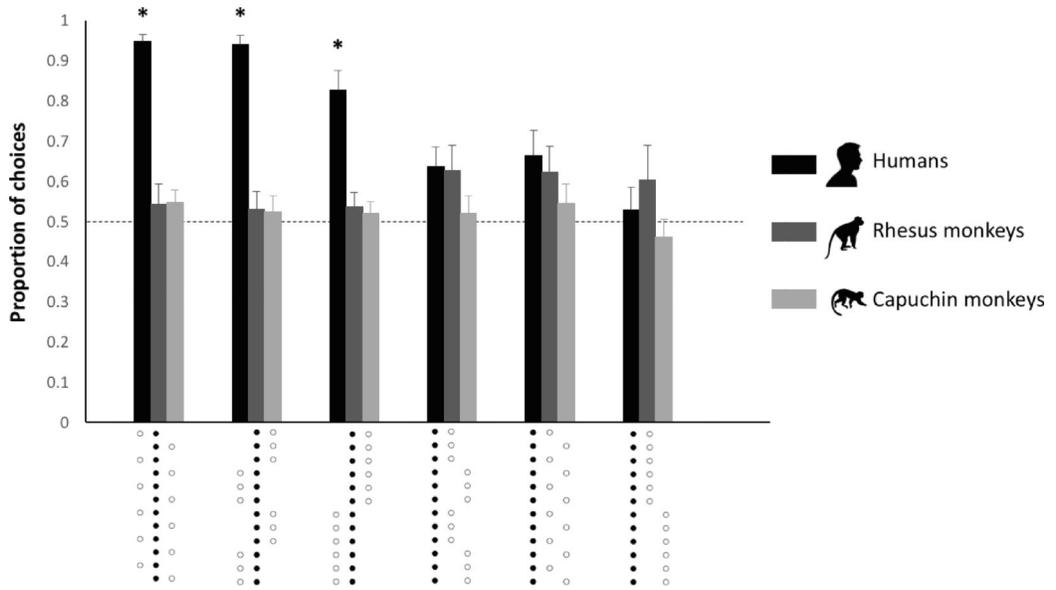
Figure 4.
Performance in the illusory probe trials, with proportion of choice for the dots comprising the better Gestalt (represented by black dots below the horizontal axis) for humans, rhesus monkeys, and capuchin monkeys. Asterisks indicate significance preference patterns. Error bars represent the standard errors.

Table 1.

Individual performances of monkeys (binomial tests, Bonferroni corrected alpha level).

Rhesus Monkey	Trials to criterion	Arrangement						Divided Clusters (1, 2, 3)	Undivided Clusters (4, 5, 6)	Overall
		1	2	3	4	5	6			
Lou	135	13/42	20/41	15/35	12/36	9/26	20/20	48/118	41/82	89/200
		$P = 0.644$	$P = 1.000$	$P = 0.500$	$P = 0.065$	$P = 0.169$	$P < 0.001*$	$P = 0.053$	$P = 1.000$	$P = 0.137$
Han	196	19/33	23/34	17/31	25/40	23/29	20/33	59/98	68/102	127/200
		$P = 0.469$	$P = 0.058$	$P = 0.720$	$P = 0.154$	$P = 0.002*$	$P = 0.296$	$P = 0.054$	$P = 0.001*$	$P < 0.001*$
Hank	5,399	18/31	12/33	22/47	18/28	17/33	15/28	52/111	50/89	102/200
		$P = 0.473$	$P = 0.163$	$P = 0.771$	$P = 0.092$	$P = 1.000$	$P = 0.851$	$P = 0.569$	$P = 0.289$	$P = 0.834$
Murph	177	20/33	12/21	22/43	26/43	20/37	6/23	54/97	52/103	106/200
		$P = 0.296$	$P = 0.664$	$P = 1.000$	$P = 0.222$	$P = 0.743$	$P = 0.035$	$P = 0.310$	$P = 1.000$	$P = 0.437$
Obi	900	22/44	13/26	27/46	22/34	19/27	14/23	62/116	55/84	117/200
		$P = 1.000$	$P = 1.000$	$P = 0.302$	$P = 0.121$	$P = 0.026$	$P = 0.202$	$P = 0.516$	$P = 0.006*$	$P = 0.019$
Chewie	1,298	19/26	20/30	22/31	37/41	29/35	27/37	61/87	93/113	154/200
		$P = 0.029$	$P = 0.099$	$P = 0.029$	$P < 0.001*$	$P < 0.001*$	$P = 0.008*$	$P < 0.001*$	$P < 0.001*$	$P < 0.001*$
Luke	550	20/40	17/38	15/30	25/40	17/27	12/25	52/108	54/92	106/200
		$P = 1.000$	$P = 0.627$	$P = 1.000$	$P = 0.154$	$P = 0.248$	$P = 1.000$	$P = 0.773$	$P = 0.117$	$P = 0.437$
Human-like perception		0/7	0/7	0/7	1/7	2/7	2/7	1/7	3/7	2/7
No bias		7/7	7/7	7/7	6/7	5/7	5/7	6/7	4/7	5/7
Reversed bias		0/7	0/7	0/7	0/7	0/7	0/7	0/7	0/7	0/7

Capuchin Monkey	Trials to criterion	Arrangement						Divided Clusters (1, 2, 3)	Undivided Clusters (4, 5, 6)	Overall
		1	2	3	4	5	6			
Gambit	3,935	14/38	32/40	24/36	18/38	12/26	12/22	70/114	42/86	112/200
		$P = 0.143$	$P < 0.001*$	$P = 0.065$	$P = 0.871$	$P = 0.845$	$P = 0.831$	$P = 0.019$	$P = 0.914$	$P = 0.104$
Gonzo	993	12/32	15/36	18/39	12/36	19/29	10/28	45/107	41/93	86/200
		$P = 0.215$	$P = 0.405$	$P = 0.749$	$P = 0.065$	$P = 0.136$	$P = 0.185$	$P = 0.122$	$P = 0.300$	$P = 0.056$
Liam	715	13/32	18/33	21/45	12/36	22/36	13/18	52/110	47/90	99/200
		$P = 0.377$	$P = 0.728$	$P = 0.766$	$P = 0.065$	$P = 0.243$	$P = 0.096$	$P = 0.634$	$P = 0.752$	$P = 0.944$
Bailey	975	20/39	16/33	15/36	22/39	17/34	12/19	51/108	51/92	102/200

	N									
Gretel	249	21/39, P = 1.000	13/24, P = 1.000	21/42, P = 0.405	19/37, P = 0.552	13/33, P = 1.000	5/25, P = 0.359	55/105, P = 0.631	37/95, P = 0.348	92/200, P = 0.834
Benny	2,313	20/31, P = 0.749	9/34, P = 0.839	24/39, P = 1.000	18/37, P = 1.000	20/30, P = 0.296	11/29, P = 0.004*	53/104, P = 0.696	49/96, P = 0.040	102/200, P = 0.289
Mason	3,417	15/31, P = 0.150	12/31, P = 0.009*	19/37, P = 0.196	20/39, P = 1.000	12/31, P = 0.099	16/31, P = 0.265	46/99, P = 0.922	48/101, P = 0.919	94/200, P = 0.834
Nkima	280	21/39, P = 1.000	12/27, P = 0.281	19/35, P = 1.000	8/30, P = 1.000	4/36, P = 0.281	5/33, P = 1.000	52/101, P = 0.547	17/99, P = 0.691	69/200, P = 0.437
Griffin	945	12/22, P = 0.749	19/29, P = 0.701	20/41, P = 0.736	20/39, P = 0.016*	22/37, P < 0.001*	11/32, P < 0.001*	51/92, P = 0.842	53/108, P < 0.001*	104/200, P < 0.001*
Widget	310	32/43, P = 0.832	25/38, P = 0.136	28/41, P = 1.000	32/54, P = 1.000	10/11, P = 0.324	7/13, P = 0.110	85/122, P = 0.348	49/78, P = 0.923	134/200, P = 0.621
Wren	926	27/37, P = 0.002*	27/39, P = 0.073	29/44, P = 0.028*	35/37, P = 0.220	11/23, P = 0.012*	8/20, P = 1.000	83/120, P < 0.001*	54/80, P = 0.031	137/200, P < 0.001*
Lily	388	19/41, P = 0.008*	19/34, P = 0.024*	16/32, P = 0.049*	23/42, P < 0.001*	16/29, P = 1.000	14/22, P = 0.503	54/107, P < 0.001*	53/93, P = 0.002*	107/200, P < 0.001*
Nala	1,610	23/38, P = 0.755	18/31, P = 0.608	12/45, P = 1.000	24/50, P = 0.644	9/14, P = 0.711	12/22, P = 0.286	53/114, P = 1.000	45/86, P = 0.213	98/200, P = 0.358
Logan	132	24/35, P = 0.256	12/39, P = 0.473	17/34, P = 0.002*	30/43, P = 0.888	17/26, P = 0.424	11/23, P = 0.832	53/108, P = 0.512	58/92, P = 0.747	111/200, P = 0.834
Human-like bias		3/14, P = 0.041*	2/14, P = 0.024*	2/14, P = 1.000	2/14, P = 0.014*	1/14, P = 0.169	0/14, P = 1.000	2/14, P = 0.923	1/14, P = 0.016	2/14, P = 0.137
No bias		11/14	10/14	11/14	11/14	12/14	12/14	12/14	12/14	11/14
Reversed bias		0/14	2/14	1/14	1/14	1/14	2/14	0/14	1/14	1/14

Table 2.

Human data (binomial tests, Bonferroni corrected alpha level).

Subject	Trials To Criterion	Arrangement						Divided Clusters (1,2,3)	Undivided Clusters (4, 5, 6)	Overall
		1	2	3	4	5	6			
1	21	13/13 $P<0.001$*	15/15 $P<0.001$*	22/23 $P<0.001$*	6/16 $P=0.454$	9/18 $P=1.000$	6/15 $P=0.607$	50/51 $P<0.001$*	21/46 $P=0.659$	71/100 $P<0.001$*
2	21	12/13 $P=0.003$*	22/23 $P<0.001$*	17/17 $P<0.001$*	16/22 $P=0.052$	13/17 $P=0.049$	4/8 $P=1.000$	51/52 $P<0.001$*	33/47 $P=0.008$*	84/100 $P<0.001$*
3	21	11/14 $P=0.057$	17/21 $P=0.007$*	10/20 $P=1.000$	12/21 $P=0.664$	9/13 $P=0.267$	7/11 $P=0.549$	38/55 $P=0.006$*	28/45 $P=0.135$	66/100 $P=0.002$*
4	26	21/23 $P<0.001$*	10/10 $P=0.002$*	13/19 $P=0.167$	10/23 $P=0.678$	3/12 $P=0.146$	6/13 $P=1.000$	44/52 $P<0.001$*	19/48 $P=0.193$	63/100 $P=0.012$
5	21	19/19 $P<0.001$*	19/19 $P<0.001$*	21/21 $P<0.001$*	9/14 $P=0.424$	7/14 $P=0.100$	5/13 $P=0.581$	59/59 $P<0.001$*	21/41 $P=1.000$	80/100 $P<0.001$*
6	37	13/13 $P<0.001$*	14/16 $P=0.004$*	13/19 $P=0.167$	8/21 $P=0.383$	11/18 $P=0.481$	2/13 $P=0.022$	40/48 $P<0.001$*	21/52 $P=0.212$	61/100 $P=0.035$
7	24	12/12 $P<0.001$*	18/18 $P<0.001$*	18/21 $P=0.001$*	11/20 $P=0.824$	6/12 $P=1.000$	9/17 $P=1.000$	48/51 $P<0.001$*	26/49 $P=0.775$	74/100 $P<0.001$*
8	21	16/17 $P<0.001$*	20/22 $P<0.001$*	14/14 $P<0.001$*	10/17 $P=0.629$	11/19 $P=0.648$	4/11 $P=0.549$	50/53 $P<0.001$*	25/47 $P=0.771$	75/100 $P<0.001$*
9	21	16/16 $P<0.001$*	17/17 $P<0.001$*	21/21 $P<0.001$*	7/13 $P=1.000$	15/18 $P=0.008$*	7/15 $P=1.000$	54/54 $P<0.001$*	29/46 $P=0.104$	83/100 $P<0.001$*
10	21	15/15 $P<0.001$*	18/18 $P<0.001$*	14/19 $P=0.064$	7/18 $P=0.481$	10/13 $P=0.092$	6/17 $P=0.332$	47/52 $P<0.001$*	23/48 $P=0.885$	70/100 $P<0.001$*
11	22	10/12 $P=0.039$	14/15 $P=0.001$*	8/27 $P=0.052$	13/14 $P=0.002$*	2/14 $P=0.013$	3/18 $P=0.008$*	32/54 $P=0.220$	18/46 $P=0.184$	50/100 $P=1.000$
12	21	18/18 $P<0.001$*	30/30 $P<0.001$*	18/18 $P<0.001$*	5/10 $P=1.000$	12/12 $P<0.001$*	9/12 $P=0.146$	66/66 $P<0.001$*	26/34 $P=0.003$*	92/100 $P<0.001$*
13	20	16/19 $P=0.004$*	11/19 $P=0.648$	9/16 $P=0.804$	16/16 $P<0.001$*	5/16 $P=0.210$	6/14 $P=0.791$	36/54 $P=0.020$	27/46 $P=0.302$	63/100 $P=0.012$
14	21	16/16 $P<0.001$*	32/32 $P<0.001$*	14/14 $P<0.001$*	4/8 $P=1.000$	16/16 $P<0.001$*	12/14 $P=0.013$*	62/62 $P<0.001$*	32/38 $P<0.001$*	94/100 $P<0.001$*

Subject	Trials To Criterion	Arrangement						Divided Clusters (1,2,3)	Undivided Clusters (4, 5, 6)	Overall
		1	2	3	4	5	6			
15	22	18/22	9/9	15/15	17/18	3/18	3/18	42/46	23/54	65/100
		$P = 0.004$*	$P = 0.004$*	$P < 0.001$*	$P < 0.001$*	$P = 0.021$	$P = 0.008$*	$P < 0.001$*	$P = 0.341$	$P = 0.004$*
16	24	19/19	16/18	18/19	17/17	12/12	14/15	53/56	43/44	96/100
		$P < 0.001$*	$P = 0.001$*	$P < 0.001$*	$P < 0.001$*	$P < 0.001$*	$P < 0.001$*	$P < 0.001$*	$P < 0.001$*	$P < 0.001$*
17	22	17/18	19/21	12/21	11/18	13/14	6/8	48/60	30/40	78/100
		$P < 0.001$*	$P < 0.001$*	$P = 0.664$	$P = 0.481$	$P = 0.002$*	$P = 0.289$	$P < 0.001$*	$P = 0.002$*	$P < 0.001$*
18	21	13/13	19/19	17/17	15/21	11/12	13/18	49/49	39/51	88/100
		$P < 0.001$*	$P < 0.001$*	$P < 0.001$*	$P = 0.078$	$P = 0.006$*	$P = 0.096$	$P < 0.001$*	$P < 0.001$*	$P < 0.001$*
19	21	19/20	20/21	11/15	18/20	12/15	4/9	50/56	34/44	84/100
		$P < 0.001$*	$P < 0.001$*	$P = 0.118$	$P < 0.001$*	$P = 0.035$	$P = 1.000$	$P < 0.001$*	$P < 0.001$*	$P < 0.001$*
20	20	19/19	17/17	22/22	10/23	11/11	8/8	58/58	29/42	87/100
		$P < 0.001$*	$P < 0.001$*	$P < 0.001$*	$P = 0.678$	$P < 0.001$*	$P = 0.008$*	$P < 0.001$*	$P = 0.020$	$P < 0.001$*
Illusory bias		18/20	19/20	12/20	5/20	7/20	3/20	18/20	7/20	16/20
No bias		2/20	1/20	8/20	15/20	13/20	15/20	2/20	13/20	4/20
Reversed bias		0/20	0/20	0/20	0/20	0/20	2/20	0/20	0/20	0/20