

# Seeing Can Be Remembering: Interactions Between Memory and Perception in Typical and Atypical Development

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## Abstract

Recent work suggests that memory representations may guide basic perceptual functions, such as figure-ground perception. In three studies we assessed top-down contributions to figure-ground perception in typical development and in two developmental disorders: Down syndrome (DS) and autism (ASD). We investigated how figure-ground segregation is modulated by high-level cues (i.e., memory representations) and low-level cues (i.e., convexity and surface integration). Study 1 results showed that both high-level and low-level contributions to figure-ground perception are functional by the age of 4 years. In Study 2, individuals with DS exhibited intact figure-ground segregation based on low level cues when compared with mental age-matched participants, but they showed attenuated effects of high-level memory cues on figure-ground assignment. In Study 3, individuals with ASD showed intact effects of both high-level and low-level cues on figure-ground perception, counter to previous suggestions that high-level influences on perception are usually impaired in ASD.

## Keywords

development, Down syndrome, autism spectrum disorders, memory, top-down influence, figure-ground perception, convexity

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Recent demonstrations of extensive interactions between neural systems involving dynamic feedforward and feedback processing loops are inconsistent with the traditional view that memory and perception are separate processes realized in dissociable neural systems (for discussion, see Barense, Ngo, Hung, & Peterson, 2012; Graham, Barense, & Lee, 2010; Lee, Yeung, & Barense, 2012; MacEvoy & Epstein, 2011; Murray & Bussey, 1999; Murray, Bussey, & Saksida, 2007; Nadel & Peterson, 2013; Peterson, 1994; Stokes, Atherton, Patai, & Nobre, 2011). For instance, it was traditionally assumed that the initial segregation of the visual field into objects (“figures”), termed “figure-ground perception,” occurs in a serial, feedforward manner (e.g., Craft, Schütze, Niebur, & von der Heydt, 2007; Zhou, Friedman, & von der Heydt, 2000), with object memories accessed only after figure assignment. It is now clear that figure-ground perception is modulated by object memories (e.g., Grill-Spector & Kanwisher, 2005; Navon, 2011; Peterson & Gibson, 1994a, 1994b; Peterson, Harvey, & Weidenbacher, 1991; Peterson &

Lampignano, 2003; Peterson & Skow, 2008; Vecera & Farah, 1997) as well as by lower-level generic cues (e.g., Peterson & Gibson, 1994b; Peterson & Salvagio, 2008).

Well-validated behavioral tasks (Barense et al., 2012; Peterson, de Gelder, Rapcsak, Gerhardstein, & Bachoud-Lévi, 2000; Peterson, Gerhardstein, Mennemeier, & Rapcsak, 1998; Peterson & Salvagio, 2008) can help us define the emergence of these various types and levels of modulation of figure-ground segregation during development. Using these tasks, we can determine how interactions across low and high levels in the visual

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stream may vary in populations known to have altered patterns of long- versus short-range brain connectivity, including Down syndrome (DS; Anderson et al., 2013) and autism spectrum disorders (ASD; e.g., Just, Cherkassky, Keller, & Minshew, 2004).

Individuals with autism have shown decreased brain network integration and altered perceptual function, leading to theories proposing reduced top-down modulation of perception in this group (Edgin & Pennington, 2005; Just, Cherkassky, Keller, Kana, & Minshew, 2007; Just et al., 2004; Mottron, Dawson, Soulières, Hubert, & Burack, 2006; Pellicano & Burr, 2012). Although early neuroimaging studies of interregional connectivity in autism reported reduced network integration (the “underconnectivity hypothesis”; Cherkassky, Kana, Keller, & Just, 2006; Jou et al., 2011; Kennedy & Courchesne, 2008; Weng et al., 2010), more recent work has suggested over- rather than underconnectivity in both short- and long-range connections in autism compared with typically developing children (Di Martino et al., 2011; Keown et al., 2013; Monk et al., 2009; Noonan, Haist, & Müller, 2009; Supekar et al., 2013). Therefore, the neural mechanisms underlying perceptual differences in autism are currently under debate (Uddin, 2015).

Pellicano and Burr (2012) used a Bayesian framework to explain the perceptual profile of autism, claiming that those with autism have a reduced influence of prior probability estimations (or “priors”). However, the nature of these priors remains ill defined. Recent theories, supported by anatomical and functional research (e.g., Clark, 2013; Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013; Nadel & Peterson, 2013), suggest that visual stream interactions involve a series of feedback loops between lower and higher cortical levels. By this view, there can be many different kinds of priors, each dependent on a different feedback mechanism. In the present study we examine a specific set of interactions across low and high levels in the visual stream involved in figure-ground segregation by using a well-validated set of tasks developed by Peterson and colleagues. These paradigms allowed us to test the contributions of priors across various levels of the visual stream in ASD and DS. Specifically, we test the use of object memory cues, likely requiring feedback from the anterior temporal lobe (perirhinal cortex; Barense et al., 2012), as well as more generic cues, such as convexity and surface integration, likely reliant on lower-level interactions occurring in more posterior areas in the visual cortex.

DS (trisomy 21) is another neurodevelopmental disorder in which examination of between-level interactions may prove useful. Edgin (2013) suggested that DS may be best viewed as a syndrome involving inefficient interregional connectivity. Consistent with this view, Anderson et al. (2013) reported evidence for higher

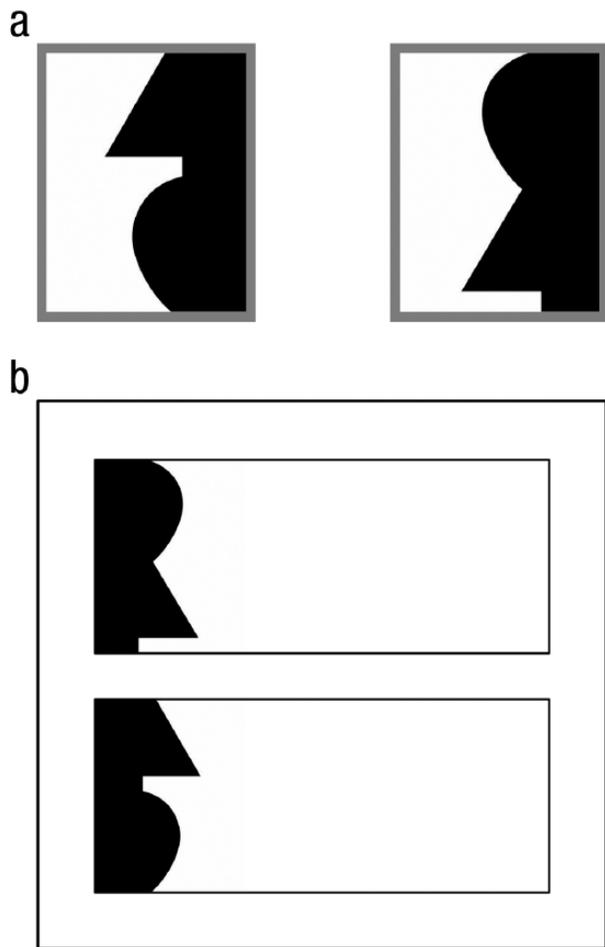
functional connectivity in short-range connections and weaker connectivity in a small subset of long-range connections in individuals with DS compared with typically developing control subjects matched by chronological age. Such alterations in connectivity could lead to differences in how information is integrated across regions. Although some studies have suggested that specific perceptual processes carried out in the ventral visual stream are unaffected in DS, including intact visual-spatial perception (Brown et al., 2003; Fidler, Hepburn, & Rogers, 2006; Pennington, Moon, Edgin, Stedron, & Nadel, 2003), research addressing top-down influences on perception is scarce and no study has examined performance on behavioral measures that specifically assess interactions across various levels of this system.

Given the evidence for abnormal brain connectivity in both ASD and DS, our aim was to examine each group’s use of both low- and high-level cues for figure ground perception. To do so, we used variants of figure-ground tests in which figure assignment depended on specific cues, each requiring integration across different levels of the ventral visual stream, as discussed next.

### High-Level Implicit Influences on Figure Assignment

The Object Memory Effects on Figure Assignment (OMEFA) test (Barense et al., 2012; Peterson et al., 1998; Peterson et al., 2000) has been used in populations with and without brain injury to measure effects of object memories on figure assignment. Object memory influences arise in high levels of the ventral processing stream (Barense et al., 2012; Peterson & Skow, 2008). The OMEFA test consists of two types of displays in which two abutting regions share a central, vertically oriented border (Fig. 1a). In *experimental displays* the region on one side of the central border depicts a portion of a well-known object; this is the critical region of the experimental displays. In *control displays*, the region on one side of the central border depicts a critical region that was created by spatially rearranging the parts of the well-known objects shown in the experimental displays into novel configurations.

In previous work employing this test, typical observers report seeing a larger percentage of the critical regions as figure in the experimental displays than in the control displays. This difference constitutes evidence that memories of objects are accessed prior to and influence figure assignment (for converging evidence, see Navon, 2011; Peterson et al., 1991; Peterson & Gibson, 1994a, 1994b; Vecera & Farah, 1997). A series of investigations has shown that object memories influence figure assignment only when they are accessed quickly, within 100–500 ms of stimulus onset (Peterson,



**Fig. 1.** (a) Object memory-based figure-ground perception test and (b) explicit familiarity discrimination test. (a) Test of effects of object memories on figure assignment. Critical regions are shown in black. For the experimental stimuli (shown on the left), the critical region portrayed a portion of a well-known object (in this case a portion of a table lamp) is portrayed by the black region to the right of the central border. For the corresponding control stimulus (shown on the right), the critical region was created by rearranging the parts of the well-known object into a novel configuration. (In the figure on the right, the critical region created by rearranging the parts of the table lamp is in black on the right of the central border.) The critical regions of both experimental and control stimuli were balanced for color (black and white) and for side (on the left and right of the central border). The participants were asked to report whether they perceived the black or white region as the figure at the central border. (b) Explicit object discrimination test. An intact configuration of a well-known object and the corresponding control part-rearranged version drawn from the OMEFA test were shown one above the other. Both were black. The critical region in the top display depicts a portion of a table lamp; the critical region in the bottom display is a novel configuration created by rearranging the parts of the table lamp. Subjects were asked to report whether the black region on the top or on the bottom portrays a well-known object (the top/bottom location was balanced).

2012; Peterson et al., 1991; Peterson & Gibson, 1994a, 1994b). In addition, Peterson et al. (2000; Peterson et al., 1991) showed that explicit object recognition is neither

necessary nor sufficient for object memories to influence figure assignment and suggested that fast access to object memories occurs automatically without awareness (i.e., implicitly).

Regarding the neural basis for these implicit effects of memory on perception, Barense et al. (2012) showed that an intact perirhinal cortex (PRC) was necessary for the typical pattern to be evident in the OMEFA task. This finding indicated that feedback from the PRC to visual cortex is necessary to discriminate both novel and familiar objects composing the same parts, a finding that was later upheld with neuroimaging evidence in typical developing adults (Peterson, Cacciamani, Barense, & Scalf, 2012).

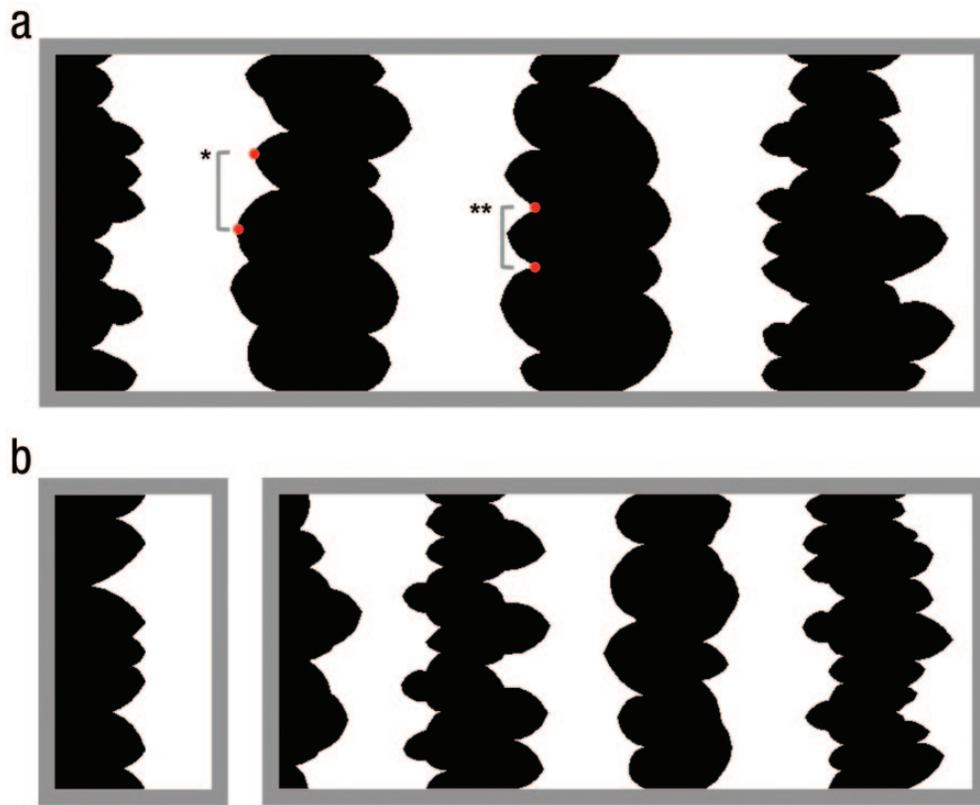
### Explicit Object Recognition

As a contrast to the implicit object memory cues guiding figure ground assignment, we also test explicit object identification, using two tasks that do not require fast access to object memories. The inclusion of these explicit tests will allow us to tease apart potential dissociations between implicit and explicit access to object representations (see the method section of Study 1 for more details). Performance on the explicit tasks can serve to situate our results with respect to the previous literature, where explicit object recognition and identification tasks have been used.

### Low-Level Influences on Figure Assignment: Convexity and Background Homogeneity Cues

To assess the influence of lower-level object properties on figure assignment, we tested figure-ground perception under conditions where a “generic” property biases figure assignment but does not require access to particular object memories. One such generic object property is convexity. Kanizsa and Gerbino (1976) showed that participants are highly likely to perceive convex regions as figures in 8-region displays in which convex regions alternated with concave regions (see Fig. 2b, right side). Responses to convexity have been observed in V4 of the ventral processing stream (Pasupathy & Connor, 1999)—at lower levels than the anterior or medial temporal regions where objects are thought to be represented.

We used both 2- and 8-region displays with alternating convex and concave regions (Figs. 2a and 2b) because Peterson and Salvagio (2008) demonstrated that convex-region-as-figure reports are substantially higher for 8-region displays than for 2-region displays. This region number effect is due to the joint operation of two priors: (a) that objects tend to be convex and (b) that single surfaces tend to be a single color (Goldreich & Peterson, 2012). The



**Fig. 2.** (a) A sample black-and-white display illustrating convex and concave regions and (b) sample displays used to assess the effects of convexity and the interaction between convexity and surface integration on figure assignment. (a) The convex regions are in black; the concave regions are in white. The red dots identify successive minima of curvature from inside the different regions. The bracket marked with an asterisk illustrates a part of a concave region, and the bracket marked by two asterisks illustrates a part of a convex region. (b) Test of effects of convexity and the interaction between convexity and surface integration on figure assignment (i.e., sample 2-region display on the left and 8-region display on the right side). In the figure, the convex regions are black and the concave regions are white. Their black/white contrast and their left/right location relative to the central border were balanced in the task. The participant was asked to say whether the black or white region appeared to be the figure at the central border.

benefit shown in convex-region-as-figure reports for 8-region displays requires both an intact response to convexity as an object cue and a spared ability to integrate disparate single color concave regions into a single surface (i.e., surface integration). These priors interact to produce perception, but this form of interaction within the visual cortex does not require feedback from higher levels where object memories are represented. The test of convexity and surface integration on figure assignment is thus an “intermediate” test of interactive processing.

In the current report we assess how figure ground segregation is affected by (a) low-level influences of convexity operating on a single border in 2-region displays, (b) intermediate-level influences involving the interaction of convexity (a local effect) and surface integration (a global effect) in 8-region displays, and (c) high-level contributions from object memories in OMEFA displays.

Three groups of participants are tested in three studies: typically developing participants spanning 4 years to adulthood (Study 1) and individuals with DS and ASD (along with their associated control samples matched by mental age) in Studies 2 and 3, respectively. In addition, we contrast performance on the OMEFA task that requires fast, implicit access to object memories with performance on explicit tests of object identification that can be accomplished with slower processing. These studies will provide insight into how contributions from different levels of the ventral visual stream are integrated in these different populations.

### Study 1: Typical Development

In Study 1 we test the development of low-, intermediate-, and high-level influences on figure-ground perception in

typically developing participants spanning 4 years of age to adulthood. Previous studies have shown that the ability to segregate between figure and background using Gestalt configural cues (e.g., common motion, alignment, and good form) emerges in typical development around 3–4 months (Johnson, 2001; Quinn & Schyns, 2003) and becomes adultlike by 8 months (Needham & Baillargeon, 1997). Yet no previous developmental studies have tested convexity as a figure cue, nor have they tested the interaction between convexity and surface integration. Nevertheless, we expect that figure assignment based on these low- and intermediate-level cues should be online early in typical development and remain stable with age. Some studies have suggested extended developmental trajectories for medial temporal lobe dependent tasks (Edgin, Spanò, Kawa, & Nadel, 2014; Golarai et al., 2007), so it is possible that object memory contributions to figure-ground perception may develop later. In contrast, implicit and explicit memories have been shown to dissociate across development, with some studies suggesting that implicit perceptual priming does not show age-related change (Graf, 1990; Perez, Peynircioğlu, & Blaxton, 1998; Rovee-Collier, 1997). Therefore, we hypothesize that we will find early developing figure-ground perception based on implicit access to object memories, whereas explicit object identification will have a more extended trajectory.

## Method

**Participants.** A total of 30 typically developing participants ranging from 4 to 19 years were recruited through a variety of means, including contact with public parent organizations and the University of Arizona undergraduate subject pool. Exclusion criteria included the presence of autistic disorder diagnosis, past head injury, and incident of loss of consciousness (greater than 5 min in length). Participants were divided into three age subgroups to examine the developmental trajectory of figure-ground perception: 10 young children (mean age = 5.01; range = 4.33–6.50 years; 6 females), 10 older children and adolescents (mean age = 13.02; range = 9.17–16.50 years; 4 females), and 10 young adults (mean age = 18.98; range = 18.17–19.58 years; 6 females). The mean Kaufman Brief Intelligence Test, Second Edition (KBIT-II) full IQ was  $110.4 \pm 8$  (range = 96–121) for young children,  $105.6 \pm 12.47$  (range = 82–126) for older children and adolescents, and  $110.6 \pm 7.46$  (range = 100–123) for young adults.

**Assessment procedures and materials.** Participants took part in a 1.5-hr testing session in a laboratory setting or in their home in a location with minimal distractions by highly experienced examiners. Each

participant first received the KBIT-II, a test of general intellectual ability, and then the test of convexity and surface integration on figure assignment, followed by the OMEFA task and the familiarity object discrimination test. The explicit object identification task was administered last, to avoid influencing performance on the OMEFA test. In Study 3, the Autism Diagnostic Observation Schedule, Second Edition (ADOS-2; Lord et al., 2012) was administered at the end of the session. All procedures were approved by the University of Arizona Biomedical Institutional Review Board.

The figure assignment tasks were presented in a child-appropriate manner, such that participants were asked to help a pilot who had embarked on a mission to Mars to identify objects in space: trees from Mars in the test of convexity and surface integration on figure assignment; novel objects from Mars and well-known objects from Earth in the OMEFA task.<sup>1</sup>

### Intelligence measure

The KBIT-II is a measure of verbal (i.e., verbal knowledge and riddles) and nonverbal (i.e., matrices) intelligence suitable for individuals from 4 to 90 years old (Kaufman & Kaufman, 2004). Standard scores for the KBIT-II have a mean equal to 100, and a standard deviation of 15.

### Figure-ground perception

This test is a measure of the tendency to use two priors for figure assignment: (a) the prior that objects tend to be convex and (b) the prior that single objects tend to be a single color. The displays are composed of either 2 or 8 alternating black and white convex and concave regions. These regions were each composed of multiple parts. Convex regions had convex (bulging outward) parts whereas concave regions were the complements of abutting convex regions and had concave parts (see Fig. 2). Convex regions and concave regions were presented equally often as black or white. Displays were presented on a medium gray backdrop with which the black and white regions contrasted equally. The stimuli were all 4.19 cm high ( $5.98^\circ$  of visual angle) and ranged from 1.89–11.02 cm in width ( $2.7^\circ$ – $15.4^\circ$ ). The test consisted of 28 unique displays for both conditions (2-region and 8-region displays, Fig. 2b). The order of administration of the 2-region and 8-region conditions was counterbalanced. The stimuli were presented individually and the participant was asked to say whether the black or white region appeared to be the figure at the central border. They were instructed that the nonfigural region would appear as a shapeless background and would seem to continue behind the shaped figure. The same instructions were used for both the 2-region and 8-region displays. The examiner explained that we were interested in how

observers perceive figures and not necessarily in correct answers. Four practice trials were included before each region number condition. The outcome measure used in this study was the percentage of figure reports indicating that the convex regions were the figures.

#### *Figure-ground perception and object memory (OMEFA test)*

This test includes a set of 48 displays to assess the effects of object memories on figure assignment. Each stimulus includes adjacent black and white regions framed in a rectangle. The set includes 24 experimental stimuli and 24 control stimuli. For the experimental stimuli, one of the 2 regions portrayed a portion of a well-known object (i.e., matched the representation of a known object in memory); this was the “critical” region (see Fig. 1a). For each experimental stimulus, a control stimulus was created by cutting the well-known object portrayed by the critical region into parts at the minima of curvature and rearranging the parts into a novel configuration. Thus, the critical regions of the control stimuli were composed of the same parts as the critical regions of the experimental stimuli, but they did not portray portions of well-known objects. The critical regions of both experimental and control stimuli were depicted equally often in black and in white and on the left and right sides of the central border. In addition, the side and color of particular critical regions were counterbalanced across participants. The participants were asked to report whether they perceived the black or white region as the figure at the central border. The stimuli were presented individually and were displayed until response. The outcome measure used in this study was the percentage of trials on which participants reported perceiving the critical regions as figure. We expect that if object memories are accessed sufficiently quickly to exert an influence on figure assignment, participants should perceive the critical regions as figure more often in experimental than control stimuli. Before taking part in the experimental trials, participants reported which region appeared to be figure on two practice trials with displays that were not used in the experiment.

#### *Explicit object recognition*

The familiarity discrimination task includes 21 trials. On each trial both an intact configuration of a portion of a well-known object and the corresponding part-rearranged control version drawn from the OMEFA test were shown one above the other in a manner designed to reduce ambiguity regarding which configuration is the figure. The critical regions were depicted in black on the left side of a rectangular display and were substantially smaller in area than the abutting white region with which they shared a border (these critical regions

were between 8.8% and 20.1% of the area of the abutting regions, see Fig. 1b). To further bias the percept, these displays were outlined by a thin black border and shown on a white backdrop so that the regions abutting the critical regions did not contrast with the backdrop. Based on contrast, small area, and expectation, the critical regions should be seen as figures in this test. Subjects were asked to choose the black region (top or bottom) that portrays a well-known object (the top/bottom location of the intact portion of the well-known object drawn from experimental stimuli was balanced). The outcome measure for this test was the percentage of trials on which the well-known configuration was identified as more familiar than the part-rearranged novel configuration. Unlike figure assignment, this task does not require that object memories be accessed quickly; nor does it require that object memories exert an influence on figure assignment. Thus, this test serves as one explicit test of access to object memories by the portions of familiar objects used in our displays once they are perceived as figures.

The explicit object identification task, a four-alternative forced choice task, assessed whether the participants were able to identify the objects depicted in the OMEFA test when they were shown under optimal conditions. On each trial, four colored photographs depicting whole objects were presented simultaneously, arranged in the four quadrants of a rectangular display. A colored photograph of each of the 24 well-known objects portrayed by the experimental stimuli (the target object) was paired with three distractors. The location of the target object was balanced across quadrants. On each trial, the examiner named the target object. The participants’ task was to point to the picture that best illustrates the object named by the examiner. We eliminated from the OMEFA analysis any stimuli in which the critical regions portrayed objects that an individual participant could not identify in this task; the part-rearranged controls of those objects were eliminated as well. Across the studies reported in this article, only individuals with DS, ASD, and children between 4 and 6.50 years old were assessed in this test because previous studies have shown that the objects were well recognized in most adults.

## **Results**

**Statistical analyses.** Analyses were completed with SPSS 20.0. The distributional properties of each measure (normality, floor/ceiling effects) were examined and the measures were confirmed to be able to be analyzed without transformation. At  $p = .05$ , we had adequate power to detect group differences with large effects (Cohen, 1992). Differences in background factors between the groups

were analyzed with *t* tests for normally distributed outcomes and with chi-square for dichotomous variables. A mixed model analysis of variance for repeated measures (ANOVA) across groups was applied to (a) the percentage of trials on which convex regions were seen as figures in the 2- and 8-region displays used to test effects of convexity and surface integration on figure assignment and (b) the percentage of trials on which participants reported perceiving the critical regions of experimental and control OMEFA displays as figure. When interactions were found, an independent samples *t* test was performed to explore the nature of the interaction. We examined group differences in explicit object discrimination by using univariate ANOVA in Study 1 and independent samples *t* tests in Studies 2 and 3. Finally, we used a multiple regression analysis to examine whether IQ and age relate to the effect of object memories on figure assignment (i.e., performance on the OMEFA task) in both DS and ASD groups.

*Descriptive measures.* There were no significant differences between age groups on the total KBIT-II test,  $t(18) = 1.03$ ,  $p = .32$ , for young children versus older children and adolescents;  $t(18) = -0.06$ ,  $p = .96$  for young children versus young adults;  $t(18) = -1.09$ ,  $p = .29$  for older children and adolescents versus young adults. Chronological age was significantly different between the three age groups ( $p < .001$ ). No difference was found for gender,  $\chi^2(2, n = 30) = 1.07$ ,  $p = .59$ .

*Figure-ground perception: convexity and surface integration.* A  $2 \times 3$  ANOVA with the number of regions in the display (2-region vs. 8-region displays) as the repeated factor and group (young children vs. older children and adolescents vs. young adults) as the between-subjects factor revealed a main effect of the number of regions in the display,  $F(1, 27) = 46.90$ ,  $p < .001$ . Participants were more likely to perceive convex regions as figures in the 8-region displays than in the 2-region displays (see Fig. 3a). There was no interaction between the number of regions in the display and age group,  $F(2, 27) = 0.35$ ,  $p = .71$ , nor was there a main effect of group,  $F(2, 27) = 1.47$ ,  $p = .25$ , thereby showing no age-related difference. Thus, effects of convexity supplemented by the integration of the concave regions into a background surface were observed in all groups.

*Figure-ground perception: object memory influences.* We tested patterns of performance in the three age groups on the OMEFA test to examine the developmental trajectory of high-level influences (i.e., the effects of object memories) on figure assignment. A  $2 \times 3$  ANOVA was conducted with the critical region type (experimental vs. control) as the repeated factor and group (young children

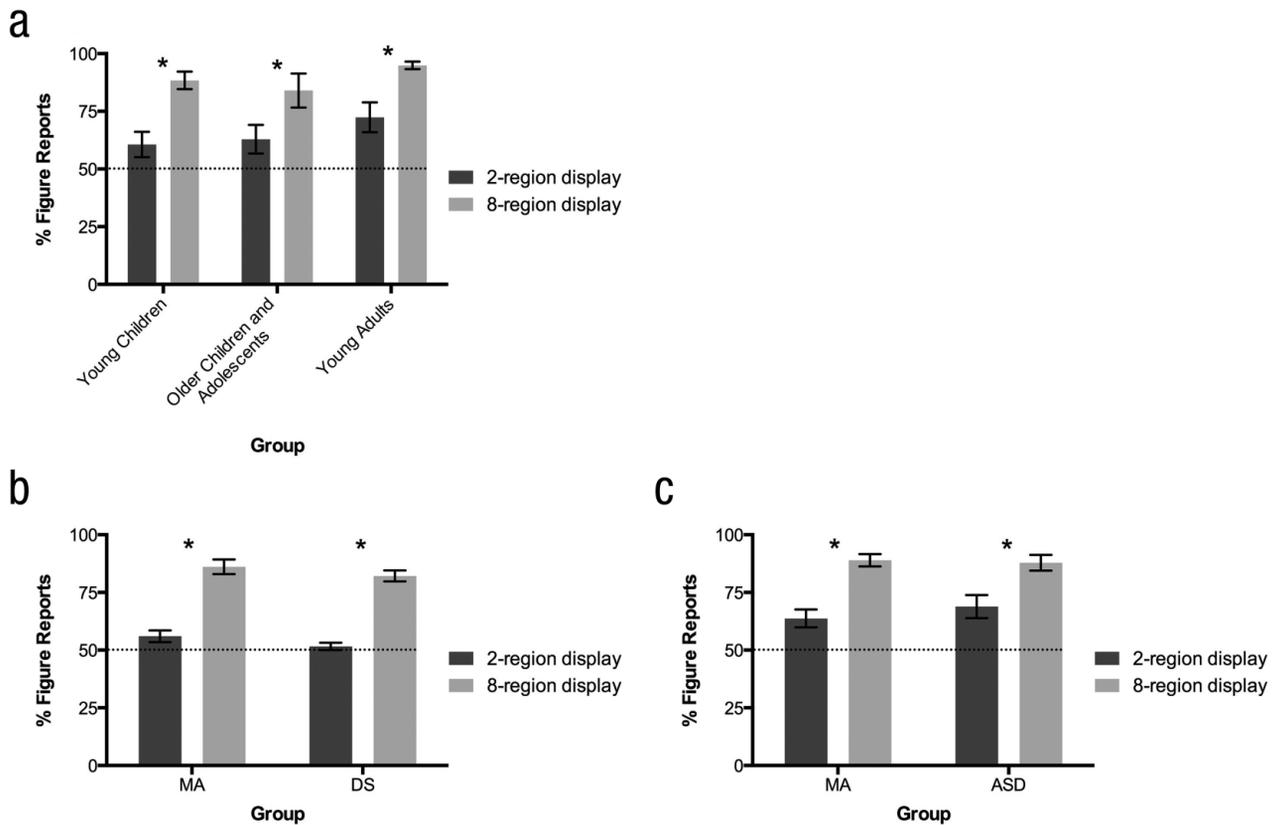
vs. older children and adolescents vs. young adults) as the between-group variable. The analysis produced significant main effects of critical region type,  $F(1, 27) = 145.69$ ,  $p < .001$ , and age group,  $F(2, 27) = 17.18$ ,  $p < .001$ . There was no interaction of critical region type  $\times$  group,  $F(2, 27) = 0.30$ ,  $p = .74$ . The main effect of region type shows that participants of all ages manifest the standard effect of object memories on figure assignment: Participants perceived the critical regions as figure more often in experimental stimuli, where they portrayed portions of well-known objects, than in control stimuli, where they depicted novel configurations created from the parts of the well-known objects (see Fig. 4a). The main effect of group shows that the percentage of critical region as figure reports increased with age, for both experimental and control displays (see Fig. 4a).

*Familiarity discrimination.* To assess group differences in explicit object recognition we compared the performance of the three groups on the familiarity discrimination test (Fig. 1b) with a one-way ANOVA. The ANOVA showed a main effect of group,  $F(2, 27) = 8.04$ ,  $p = .002$ . Further analyses were conducted to explore the main effect by using independent samples *t* tests. The younger group ( $M = 73\%$ ,  $SD = 9.55$ ) correctly discriminated the well-known objects from the part-rearranged novel objects when presented together significantly less often than older children and adolescents ( $M = 83.2\%$ ,  $SD = 8.89$ ),  $t(18) = -2.47$ ,  $p = .02$ , and young adults ( $M = 87.7\%$ ,  $SD = 6.45$ ),  $t(18) = -4.04$ ,  $p = .001$ . Object discrimination in older children and adolescents and young adults did not differ significantly,  $t(18) = -1.30$ ,  $p = .21$ . These results show that younger children are less able than are older children and young adults to distinguish between intact portions of well-known configurations and their part-rearranged control configurations when asked to explicitly report which is more familiar.

*Explicit object identification.* Almost all the younger children could identify the target objects among sets of four colored photographs when presented with the label ( $M = 99.6\%$ ,  $SD = 1.26$ ). Those few objects that subjects erred on in this task (and their part rearranged controls) were removed from the OMEFA results as discussed previously. Participants in the older children/adolescent group and the older group were not given the control identification task.

## Interim discussion

Study 1 shows that children as young as 4 years of age can use both lower-level (convexity and surface integration) and higher-level object properties (object memories) for figure-assignment in a manner similar to older children/



**Fig. 3.** Performance on the test of effects of convexity and the interaction between convexity and surface integration on figure assignment in Studies 1, 2, and 3. Error bars represent standard error of mean. (a) Percentage of figure reports of the critical regions (based on convexity and surface integration) for both 2- and 8-region displays shown as a function of group: younger children, older children and adolescents, and younger adults. (b) DS group compared with MA control group: for the two groups we report the percentage of figure reports of the critical regions (based on convexity and surface integration) for both 2- and 8-region displays. (c) ASD group compared with MA control group.

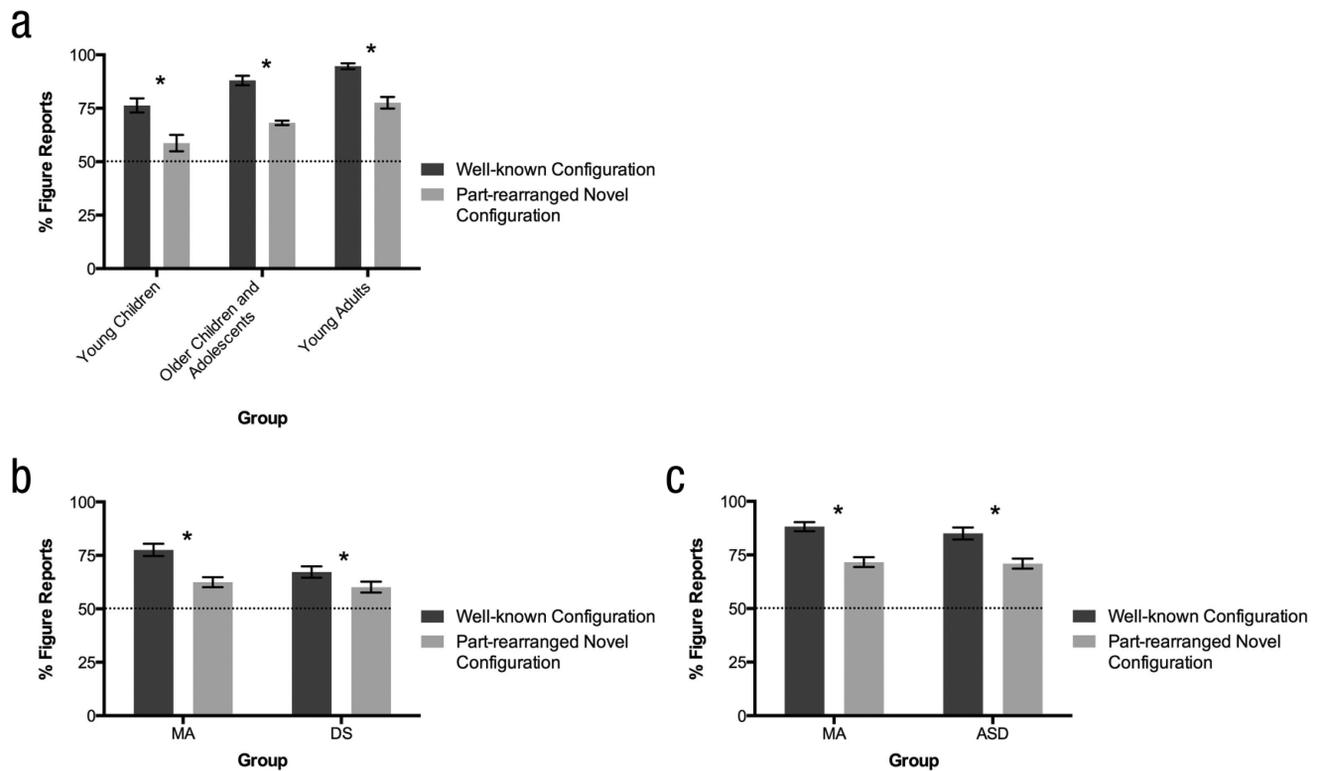
adolescents and young adults. Participants in all three age groups were more likely to perceive convex regions as figure in 8-region than in 2-region displays, thereby demonstrating that young children can use the convexity and surface integration priors for figure assignment. Participants in all three age groups were also more likely to perceive critical regions of OMEFA stimuli as figures in experimental stimuli than control stimuli, showing that memories of familiar objects exert an influence on figure assignment. There was no interaction with age, suggesting the size of this effect was consistent in each age group. Yet, the likelihood of perceiving critical regions as figures in both control and experimental stimuli increased with age. This finding may reflect either an increasing role of protrusion in figure assignment with age (as the critical regions of experimental and control stimuli were matched on this variable, but the abutting regions were not), or an increasing role of familiarity independent of configuration (i.e., familiar parts as well as familiar configurations).

Although it appears that these implicit influences on figure assignment remain stable across age, performance on one of the explicit object recognition tasks did change

across age groups. Although younger children can almost perfectly identify full color pictures of these objects, they showed more difficulty than older children or young adults on the familiarity discrimination task, which may reveal some developmental trends in the abilities tapped by this task (for further discussion, see the general discussion). In summary, the results of Study 1 suggest three sets of implicitly operating visual system “priors” (convexity, surface integration, and object memory) may be online as early as four years of age and stable across development. Study 2 and Study 3 test the integrity of these visual system priors in two syndromes influencing the ventral visual stream and network interactions (DS and autism).

## Study 2: Down Syndrome

In Study 2, we tested individuals with DS, a population with known weakened long-range connectivity, on figure-ground perception. Given this hypothesized connectivity profile (Anderson et al., 2013), we expected that children with DS would demonstrate impaired



**Fig. 4.** Performance on the OMEFA test in Studies 1, 2, and 3. Error bars represent standard error of mean. (a) The percentage of figure reports for the critical regions of experimental displays containing well-known configurations of objects and control displays containing part-rearranged novel versions of these objects shown as a function of age group. (b) DS group compared with MA control group on the OMEFA test. For the two groups we report the percentage of figure reports of the critical regions of the displays containing well-known configurations of objects and displays containing part-rearranged novel versions of these objects. Subsequent analysis produced a significant interaction of Critical Region  $\times$  Group,  $F(1, 48) = 5.6, p = .02$ . (c) ASD group compared with MA control group on the OMEFA test.

figure-ground judgments requiring interactions between memory and perception, whereas their use of lower-level generic cues to segregate figure from ground might remain intact. Despite our hypothesis of impaired implicit object memory, we did not expect to find impairments in explicit object recognition based on reports of a relatively spared ability to explicitly identify objects (Mosse & Jarrod, 2011).

## Method

**Participants.** A total of 25 individuals with DS (mean age = 16.01; range = 10.25–24 years; 13 females) were recruited through local and parent organizations and advertisement in Tucson and Phoenix, Arizona. The study had 80% power to detect medium to large effect sizes for between-group differences, corresponding to the size of effect we expected from memory task findings in the previous literature (Cohen, 1992; Pennington et al., 2003). Exclusion criteria included the presence of Robertsonian translocation, mosaicism, autistic disorder diagnosis, past head injury, or incident of loss of consciousness (greater than 5 min in length). The mean

KBIT-II full IQ of the DS sample was  $46.08 \pm 9.25$  (range = 40–79). Of the children with DS, 13 had corrected vision and 12 had no vision defects. DS (trisomy 21) was queried through parent report and verified by karyotype report or medical records. A comparison sample included 25 typically developing mental age (MA) matched children (mean age = 4.59; range = 4.08–6.50 years; 9 females). The mean KBIT-II full IQ of the comparison sample was  $111.48 \pm 10.42$  (range = 89–129). A subset of the MA-matched children overlapped with the typically developing participants tested in Study 1.

**Assessment procedures and materials.** The materials and procedure were the same as Study 1.

## Results

**Descriptive measures.** The mean raw score for the verbal and nonverbal IQ (KBIT-II) of the sample with DS was  $28.96 \pm 9.80$  and  $15.12 \pm 4.99$ , respectively. For the MA control group the mean raw score for the verbal and nonverbal IQ (KBIT-II) was  $29.32 \pm 6.96$  and  $15.04 \pm 4.3$ . The groups did not differ on the matching variable of

KBIT-II verbal,  $t(48) = -0.15, p = .88$ , and nonverbal raw scores,  $t(48) = 0.06, p = .95$ , or in gender,  $\chi^2(1, n = 50) = 1.30, p = .25$ ). Chronological age was significantly different between the DS and MA groups ( $p < .001$ ).

**Figure-ground perception: convexity and surface integration effects.** A  $2 \times 2$  ANOVA with number of regions in the display (2-region vs. 8-region displays) as the repeated factor and group (DS vs. MA) as the between-subjects factor revealed a main effect of the number of display regions,  $F(1, 48) = 207.37, p < .001$ . Effects of convexity and of the integration of the convexity cue and the surface integration cue were observed in both groups: Both DS and MA were more likely to perceive convex regions as figures in the 8-region displays than in the 2-region displays (see Fig. 3b). There was no interaction between the number of display regions and group,  $F(1, 48) = 0.007, p = .93$ , nor was a main effect of group observed,  $F(1, 48) = 2.22, p = .14$ . Thus, low-level effects of convexity and intermediate-level effects of surface integration combined with convexity are relatively spared in individuals with DS.

**Figure-ground perception: object memory influences.** We compared the group with DS to MA-matched children on the effects of object memories on figure assignment. To do so we performed a  $2 \times 2$  ANOVA with the critical region type (experimental vs. control displays) as the repeated factor and group (DS vs. MA) as the between-group variable. The analysis produced a significant main effect of critical region type,  $F(1, 48) = 42.09, p < .001$ , and a significant interaction of critical region type  $\times$  group,  $F(1, 48) = 5.6, p = .02$ . In addition, the main effect of group was marginally significant,  $F(1, 48) = 3.74, p < .06$ . Additional comparisons were conducted to explore the interaction. As Figure 4b shows, both the MA control,  $t(24) = 7.07, p < .001$ , and the DS participants,  $t(24) = 2.64, p = .01$ , perceived the critical regions as figure more often in the experimental stimuli than in the control stimuli, but this difference was attenuated in DS (7.04% DS; 15.12% MA). The difference between the groups follows from the fact that the group with DS perceived the critical regions portraying portions of well-known objects as figure significantly less often than the MA control group did,  $t(48) = -2.65, p = .01$ , whereas the two groups did not differ in perceiving the matched regions portraying novel configurations as figure,  $t(48) = -0.66, p = .51$ . Thus, higher-level influences from object memories on figure assignment are attenuated in DS individuals compared with the MA comparison group.

**Familiarity discrimination.** Familiarity discrimination in the DS group ( $M = 69.68\%, SD = 12.73$ ) and MA control group ( $M = 64.92\%, SD = 15.35$ ) did not differ significantly,  $t(48) = 1.19, p = .24$ . They showed a similar

ability to determine which figure was more familiar when asked to explicitly compare a well-known and a novel configuration.

**Explicit object identification.** An independent samples  $t$  test showed that the percentage of correct responses did not differ in the two groups when participants were asked to choose the full color object (DS group:  $M = 98.84\%, SD = 3.74$ ; MA control group:  $M = 98.4\%, SD = 2.83$ ),  $t(48) = 0.47, p = .64$ .<sup>2</sup> Thus, as expected, DS individuals were not impaired in explicit object recognition.

**Influence of age and IQ on OMEFA performance.** Multiple regression was used to investigate whether IQ and age related to the effects of object memories on figure assignment. The regression model was not significant,  $R^2 = .09, F(2, 22) = 1.06, p = .36$ , and IQ did not significantly predict the effect of object memory ( $\beta = 0.29, p = .17$ ), nor did age ( $\beta = 0.08, p = .70$ ).

### Interim discussion

These results suggest that individuals with DS have a specific deficit in a particular form of high-level influence on perception—the implicit effect of object memories on figure-ground assignment. In contrast, their explicit object recognition is intact: Individuals with DS can identify a full color object named by the experimenter from among a set of four objects (explicit object identification), and choose the well-known object from two silhouettes composed of the same parts (familiar object discrimination). Their use of lower-level properties such as convexity and surface integration for figure-ground perception is relatively intact. These findings were not related to either IQ or age.

### Study 3: Autism Spectrum Disorder

In Study 3, we test groups with ASD and their associated control samples matched by mental age. We expected that figure-ground perception using low- and intermediate-level cues would also be intact in individuals with autism. Despite the often-reported visual abnormalities in autism (e.g., Mottron et al., 2006), previous studies have found that early visual areas are typically organized and that the well-documented visual abnormalities in this population might result from altered top-down processes (e.g., Hadjikhani et al., 2004). The previous literature did not support a clear prediction regarding object memory contributions to figure assignment in individuals with autism. Earlier claims of underconnectivity in this group and reduced “top-down” influences might suggest attenuated influences of high-level cues on figure-ground perception as measured in the OMEFA task. However, more recent evidence has called into question the early results

suggesting underconnectivity (reviewed in Uddin, 2015), and therefore we might expect to find little to no difference in object memory influences on figure assignment in children with ASD compared with typically developing children. Finally, based on previous studies suggesting relative similar profiles of implicit and explicit memory (Renner, Klinger, & Klinger, 2000), we do not expect to find a dissociation between explicit and implicit versions of this task.

## Method

**Participants.** A total of 23 individuals with ASD (mean age = 15.47; range = 7.08–23.58 years) were recruited from local autism research and resource centers in the Tucson and Phoenix, Arizona, areas. The sample included 19 males and 4 females. This ratio is representative of the population, as ASD is 5 times more likely in males than in females (Centers for Disease Control and Prevention, 2008). Of the participants in the study, 11 individuals had no vision loss and 12 individuals had corrected vision. Exclusion criteria included past brain trauma or any incident of unconsciousness for greater than 5 min. All individuals who participated in the study had been diagnosed by a physician with criteria of the fifth edition of the *Diagnostic and Statistical Manual of Mental Disorders* (American Psychiatric Association, 2013), and this diagnosis was confirmed for this study with the administration of the ADOS-2 (Lord et al., 2012) by a research reliable experimenter. This clinical assessment involves the observation and evaluation of social and communicative behaviors, as well as restricted interests and repetitive behaviors. All individuals who participated in the study met the autism spectrum cutoff for the module they were administered (Lord et al., 2012). Intelligence was measured using the KBIT-II. The mean IQ of the ASD sample was  $94.17 \pm 28$  (range = 40–130). Participants were matched to mental age (MA) children ( $n = 23$ ; mean age = 14.52; range = 4.17–20.92 years; 11 females) on the verbal and nonverbal raw scores of the KBIT-II test. The mean full KBIT-II IQ of the MA sample was  $100 \pm 12.83$  (range = 80–126). Some, but not all, of the MA-matched children overlapped with the typically developing participants tested in Studies 1 and 2.

**Assessment procedures and materials.** The measures and the procedure were the same as Study 1, with the exception of the ADOS-2 administration after all other measures.

## Results

**Descriptive measures.** The mean KBIT-II verbal and nonverbal raw scores in the ASD group were not

different from a typical comparison group, verbal: ASD =  $65.22 \pm 27.10$ , MA =  $68.39 \pm 23.95$ ,  $t(44) = 0.42$ ,  $p = .68$ ; nonverbal: ASD =  $30.83 \pm 12.44$ ; MA =  $31.09 \pm 10.43$ ,  $t(44) = 0.07$ ,  $p = .94$ , and chronological age did not differ,  $t(44) = -0.6$ ,  $p = .55$ . A significant difference was found for gender,  $\chi^2(1, n = 46) = 4.85$ ,  $p = .03$ , and in the following analyses of group differences we controlled for this difference.<sup>3</sup> An examination of the differences between females and males in the ASD group in the outcome measures of main interest showed no gender differences on any outcome assessment:  $t(21) = 0.53$ ,  $p = .60$ , on the 2-region convexity display,  $t(21) = 0.18$ ,  $p = .86$ , on the 8-region convexity and surface integration display,  $t(21) = 0.93$ ,  $p = .36$ , or on the OMEFA test,  $t(21) = 0.20$ ,  $p = .84$ .

**Figure-ground perception: convexity and surface integration effects.** A  $2 \times 2$  ANOVA with number of regions in the display (2-region vs. 8-region displays) as the repeated factor and group (ASD vs. MA) as the between-subjects factor revealed a main effect of the number of regions in the display,  $F(1, 44) = 69.71$ ,  $p < .001$ . Effects of convexity and of the integration of the convexity cue and the surface integration cue were observed in both groups: Both ASD and MA were more likely to perceive convex regions as figures in the 8-region displays than in the 2-region displays (see Fig. 3c). There was no interaction between the number of regions in the display and group,  $F(1, 44) = 1.38$ ,  $p = .25$ , nor was a main effect of group observed,  $F(1, 44) = 0.18$ ,  $p = .67$ .

**Figure-ground perception: object memory influences.** A  $2 \times 2$  ANOVA with repeated measures was carried out on the percentage of trials on which participants reported perceiving the critical region as figure. The repeated factor was the critical region type (experimental vs. control) and the between-group factor was group (ASD vs. MA). The analysis produced a significant main effect of the critical region type,  $F(1, 44) = 121.94$ ,  $p < .001$ . There was neither a main effect of group,  $F(1, 44) = 0.38$ ,  $p = .54$ , nor a significant interaction of critical region type  $\times$  group,  $F(1, 44) = 0.8$ ,  $p = .38$ . Both MA control and ASD perceived the critical regions of experimental stimuli as figure more often than critical regions of control stimuli. Thus, both groups showed top-down effects of implicit, fast access to object memories on figure assignment (see Fig. 4c).

Given that the ASD and MA groups differed in gender we controlled for gender in figure assignment for the OMEFA test (both critical region types as dependent variables). An ANCOVA (between-subjects factor: group [ASD, MA]; covariate: gender) revealed no main effects of group,  $F(1, 43) = 0.19$ ,  $p = .67$ , or gender,  $F(1, 42) = 0.2$ ,  $p = .65$ , and no interaction between gender and critical region type,  $F(1, 43) = 0.21$ ,  $p = .65$ .

**Familiarity discrimination.** Object discrimination in the ASD group ( $M = 79.43\%$ ,  $SD = 12.19$ ) and MA control group ( $M = 80.43\%$ ,  $SD = 10.36$ ) did not differ significantly,  $t(44) = 0.3$ ,  $p = .77$ , showing that the ASD group has an intact ability to explicitly distinguish between a portion of a well-known configuration and a novel configuration created by spatially rearranging the parts of the familiar configuration.

**Explicit object identification.** The participants with ASD showed near-perfect performance on this task ( $M = 99.65\%$ ,  $SD = 1.67$ ), and thus demonstrated good recognition of the full color objects.<sup>4</sup>

**Influence of age and IQ on OMEFA performance.** As in Study 2, multiple regression analysis was used to test whether IQ and age are significantly related to the object memory effects on figure-ground perception for individuals with ASD (the larger percentage of reports of critical regions as figure in experimental than in control displays in the OMEFA task). With these predictors the model was not significant,  $R^2 = .08$ ,  $F(2, 20) = 0.86$ ,  $p = .44$ , and neither IQ ( $\beta = 0.28$ ,  $p = .21$ ) nor age ( $\beta = 0.06$ ,  $p = .80$ ) related to the object memory effects.

To further assess differences due to IQ levels we divided the ASD group into low functioning individuals with ASD (LF;  $n = 8$ , mean IQ = 57) and high functioning (HF) ASD ( $n = 19$ , mean IQ = 107), with similar chronological ages,  $t(25) = 0.27$ ,  $p = .79$ . We conducted a repeated measures ANOVA on the percentage of trials for which participants reported perceiving the critical region as figure in the OMEFA task with the between subjects factor of group and the repeated factor of critical region type (experimental vs. control). The LF ASD group perceived the critical regions as figure more often in the experimental stimuli ( $M = 80.5\%$ ,  $SD = 17.80$ ) than in the control stimuli ( $M = 65.25\%$ ,  $SD = 10.39$ ),  $t(7) = 2.84$ ,  $p = .02$ , similarly to the HF ASD group ( $M = 83.2\%$ ,  $SD = 14.58$  and  $M = 72.2\%$ ,  $SD = 11.6$ , respectively),  $t(18) = 3.88$ ,  $p = .001$ . Finally, the two groups did not differ in perceiving the critical regions portraying portions of well-known objects as a figure in the experimental stimuli,  $t(25) = -0.42$ ,  $p = .68$ ; nor did they differ in perceiving the matched regions portraying novel configurations in the control stimuli as a figure,  $t(25) = -1.46$ ,  $p = .16$ .

**Comparing OMEFA performance in DS and ASD groups.** To directly compare the groups in Studies 2 and 3, we conducted a subanalysis to compare 13 individuals with DS to an age, gender, and IQ raw score equivalent group of individuals with ASD ( $n = 9$ ) on the effects of object memories on figure assignment. The two groups were statistically equivalent in age (ASD mean = 14.7 years; DS mean = 17.8 years),  $t(20) = 1.47$ ,  $p = .16$ , gender

(ASD = 7 males; DS = 6 males),  $\chi^2(1, n = 22) = 2.2$ ,  $p = .2$ , verbal (ASD mean = 48.56; DS mean = 34.62),  $t(20) = -1.27$ ,  $p = .24$ , and nonverbal raw scores on the KBIT-II (ASD mean = 25.22; DS mean = 16.15),  $t(20) = -1.77$ ,  $p = .11$ . We performed a  $2 \times 2$  ANOVA with the critical region type (experimental vs. control displays) as the repeated factor and group (DS vs. ASD) as the between-group variable. The analysis showed a significant main effect of critical region type,  $F(1, 20) = 23.76$ ,  $p < .001$ , and a significant interaction of critical region type  $\times$  group,  $F(1, 20) = 10.13$ ,  $p = .005$ , with a significant main effect of group,  $F(1, 20) = 6.75$ ,  $p = .02$ . Although the ASD group perceived the critical regions as figure more often in the experimental stimuli ( $M = 86.3\%$ ,  $SD = 11.37$ ) than in the control stimuli ( $65.4\%$ ,  $SD = 9.6$ ),  $t(8) = 5.14$ ,  $p = .001$ , the subgroup of DS participants,  $t(12) = 1.34$ ,  $p = .21$ , did not show this difference ( $M = 67\%$ ,  $SD = 12.6$ ; and  $M = 62.6\%$ ,  $SD = 11.6$ , respectively). Individuals with DS perceived the critical regions in the experimental stimuli as figures significantly less often than the ASD group did,  $t(20) = -3.68$ ,  $p = .01$ , whereas the two groups did not differ in perceiving the matched regions portraying novel configurations as figure in the control stimuli,  $t(20) = -0.6$ ,  $p = .56$ . Although limited in sample size, the results of subanalysis suggest that high-level influences from object memories on figure assignment are attenuated in individuals with DS, but not in those with ASD.

### Interim discussion

In line with previous studies in basic visual perception in this population, individuals with ASD did not exhibit any difficulty with figure-ground perception based on low-level properties such as convexity and surface integration. Given inconsistent patterns in the literature regarding top-down modulation of perception in autism and the patterns of brain connectivity that can support top-down modulation, we had competing hypotheses regarding the pattern of performance that would be observed on the OMEFA task in individuals with ASD. In contrast to individuals with DS, the group with autism was not different in comparison to MA-matched participants in figure-ground perception based on object memories. Age and IQ did not predict the results obtained in the ASD group. Therefore, the findings in the DS group are not likely explained by the group's relatively lower IQ, as we should have seen an interaction between IQ level and critical region type in ASD (and DS) if that were the case. Intact influences on figure-ground perception of previous memory representations in individuals with ASD were also observed when we directly compared their performance to the DS sample, suggesting that DS shows attenuated top-down influences of object memories in comparison to ASD and controls.

Finally, individuals with ASD can recognize the full color objects and can successfully choose the well-known object from two silhouettes composed of the same parts (one portraying the parts as they are typically arranged in the well-known configuration, the other portraying the parts spatially rearranged to form a novel configuration). These results suggest that at least for these object memory-dependent tasks there is no deficit in individuals with autism.

## General Discussion

The traditional boundary between memory and perception is disappearing; recent evidence suggests that object memories can influence our initial percepts of the world, including figure-ground perception. Object memories are one form of “prior knowledge,” which could vary in syndromes or conditions with deficits in “top-down” feedback. In the current study we show that not all prior knowledge is equal—despite impairments in other effects of prior knowledge on perception in autism (e.g., Ropar & Mitchell, 2002), top-down influences on figure-ground perception are relatively proficient. Yet top-down influences on figure-ground perception are impaired in individuals with DS. Effects of other types of prior knowledge—for example, that objects tend to be convex and that single objects tend to be one color—on perception are intact in the two groups.

In Study 1, we examined the cross-sectional age-related changes in the interaction between top-down and bottom-up processing streams, operationalized in figure-ground organization based on low-level and high-level object properties, respectively. As predicted from previous research, we found that children as young as 4 years of age were able to use bottom-up properties (i.e., convexity and surface integration) for figure assignment, and this ability remained stable across age. By the age of 8 months infants are known to use other configural and Gestalt cues to segregate figure from ground (Johnson, 2001; Needham & Baillargeon, 1997; Quinn & Schyns, 2003). However, this is the first study to demonstrate that children as young as 4 years can use both convexity and surface integration cues for figure assignment. In addition, we found that object memory effects on figure assignment come online as early as 4 years and remain stable across development. Despite the age-related increase in the likelihood of seeing both types of critical regions in the OMEFA task as figure, object memory effects—measured by the difference between the percentage of trials on which regions depicting well-known objects versus novel configurations composed of the same parts are perceived as figures—did not change with age. In fact, the use of parts and whole objects both

showed age-related change at equivalent rates, leading us to believe there is stability in the use of object cues after 4 years. Although the neural correlates of these developments would need to be examined through future functional neuroimaging studies, these results suggest that the long-distance communication necessary for implicit object memory effects on figure assignment is online by at least 4 years of age in typically developing children.

Despite the continuity observed in the implicit influence of object memory on figure-ground perception, young children performed significantly worse than older children and young adults in the familiarity discrimination task that assessed their ability to explicitly distinguish between the same well-known objects and novel configurations composed by spatially rearranging the same parts. The poor performance on this test might be due to the presence of the three straight bounding edges of the two regions participants compare in this task; those edges do not correspond to the real bounding edges of the depicted objects (i.e., they are “extrinsic contours”; Nakayama, Shimojo, & Silverman, 1989), which can interfere with and slow down explicit object recognition (Gerbino & Salmaso, 1987; Rensink & Enns, 1998). In contrast, implicit effects of object memories, as measured by the OMEFA test, can operate selectively along the articulated portion of the bounding contours only (Peterson, 2003). The silhouettes used in the familiarity discrimination task lack surface detail, which makes the explicit task difficult and may provide a more sensitive index of developmental change than the easier explicit object identification task, which uses full color photographs of objects. Accurate performance on the familiarity discrimination task requires participants to treat the three straight edges bordering the critical regions as extrinsic to the depicted objects (cf. Gerbino & Salmaso, 1987; Nakayama et al., 1989), an ability that may develop with age. Finally, by design, the two stimuli presented on each trial are composed of the same collection of parts in different spatial arrangements. We note that brain damage can selectively interfere with the ability to represent the spatial relationships between parts as opposed to the parts themselves (e.g., Behrmann, Peterson, Suzuki, & Moscovitch, 2006). Moreover, Behrmann et al. (2006) found that adults are less accurate in discriminating learned objects from part-rearranged foils than from foils composed of different parts (although their performance was quite good overall). Thus, the familiarity discrimination task revealed a developmental trend in this ability, as tested in an explicit task, but not as tested implicitly by the OMEFA task.

In Study 2, we found no evidence for low-level perceptual impairments in individuals with DS, a finding

consistent with previous research in this population (Brown et al., 2003; Fidler et al., 2006). The DS group showed similar patterns of performance as their MA control sample on the test of effects of convexity and the interaction between convexity and surface integration on figure assignment. Both groups reported perceiving the regions with convex parts as the figure significantly more often than the regions with concave parts. In addition, individuals with DS perceived the convex regions as figures more in 8-region than in 2-region displays, suggesting unimpaired integration of neural inputs across local areas of visual cortex (Goldreich & Peterson, 2012; Peterson & Salvagio, 2008).

Although the findings regarding lower-level cues suggested relatively intact function, effects of high-level object memories on figure-ground perception were reduced in the sample of individuals with DS compared with their MA-matched participants. This difference was obtained despite the fact that the MA comparison had substantially fewer years of experience with visual stimuli and objects in the world than the DS group. The current study's results in the DS group are not solely due to IQ level as IQ did not relate to the object memory effects in DS or in ASD, and a direct comparison of participants with DS and ASD found attenuated ability to use object memories to guide figure assignment in the DS group only.

One potential mechanism underlying this difference in DS comes from studies conducted in typical adults. In adults, object memories must be accessed quickly to exert an influence on figure assignment. Peterson et al. (1991; Peterson & Gibson, 1994a, 1994b) tested access time by using displays that portray well-known objects in their familiar upright orientation versus an inverted orientation (i.e., rotated 180° from their familiar orientation). This orientation manipulation allowed the researchers to vary familiarity while holding constant other properties relevant to figure assignment. Effects of object memory on figure assignment were substantially reduced for inverted displays compared with upright displays. Because access to object memories is delayed for inverted versions of well-known objects (estimates vary between 100–500 ms; Jolicoeur, 1988; Perrett, Oram, & Ashbridge, 1998; Tarr & Pinker, 1989), Peterson and colleagues concluded that object memories influence figure assignment only when they are accessed quickly (Peterson et al., 1991; Peterson & Gibson, 1994a, 1994b). Evidence of fast access to memory representations (within 106 ms of stimulus onset) also comes from event-related potential studies (Sanguinetti, Allen, & Peterson, 2014; Sanguinetti, Trujillo, Schynner, Allen, & Peterson, 2014; Trujillo, Allen, Schynner, & Peterson, 2010). Other studies show that conscious object recognition is neither necessary nor sufficient for object memory influences on figure-ground

perception (Peterson et al., 2000). Taken together, these studies suggest that preexisting representations of well-known objects are typically accessed quickly and automatically to guide figure-ground perception.

The findings of our study suggest that these rapidly operating high-level influences are online by 4 years in typical development and are attenuated in DS. We know that individuals with DS can access object memories in paradigms less reliant on rapid access to object memories (i.e., explicit object discrimination), so one possibility is that rapid interactions between the brain areas that mediate high-level influences on figure-ground perception are impaired in this group. More work is needed to understand what is limiting the performance of individuals with DS on this task, including functional neuroimaging studies of interactions across the ventral visual stream. The current findings set the stage for such a study through the use of a well-characterized and well-powered sample tested on a number of behavioral tasks specifically designed to tease apart these processes.

In Study 3, we found that figure-ground segregation modulated by both (a) low- and intermediate-level properties of convexity and surface integration and (b) high-level object memories was intact in individuals with autism. The ASD group showed similar patterns of performance in both 2-region and 8-region displays, in comparison to the MA control sample: perceiving the regions with convex parts as the figure significantly more often than the regions with concave parts, and also showing the context effect (8-region display > 2-region display). Thus, individuals with ASD, similarly to the DS group, show intact use of convexity and context to segregate figure from ground, an ability that seems to emerge very early in development. Individuals with ASD—compared with the MA control group—also exhibited no differences in object memory influences on figure assignment as well as in the ability to explicitly identify objects.

Our results can inform previous notions positing altered Bayesian “priors” as an important mechanism underlying autism (Pellicano & Burr, 2012). The current study shows that the operation of some priors is spared in autism. One possibility consistent with our results is that “priors” may be operating across a number of levels, with some levels of interaction affected more than others across different developmental disorders. In this study we focused on particular interactions that have been found to occur within the ventral visual stream and medial temporal lobe subregions (e.g., Barense et al., 2012). However, interactions occur across a number of brain regions, both over short (i.e., within visual cortex, V1 to LOC; see S. O. Murray, Kersten, Olshausen, Schrater, & Woods, 2002; Nadel & Peterson, 2013) and long ranges (frontal to visual cortex; see Panichello, Cheung, & Bar,

2012; and PRC to V2, see Barense et al., 2012; Peterson et al., 2012). Although we found no deficits in high-level contributions from object memories or lower level configural cues on figure assignment in those with ASD, our results do not rule out the possibility that other types of interregional communication (e.g., frontal to visual cortex) could be less efficient in this group. Past studies have proposed weak, or attenuated, top-down feedback to explain reduced perception of visual illusions and enhanced veridical perception in ASD individuals (Mitchell, Mottron, Soulières, & Ropar, 2010; Mottron et al., 2006; Müller & Nussbeck, 2008; Pellicano & Burr, 2012; Ropar & Mitchell, 2002). Given the current study's data, we suggest the neural basis of these effects may reside outside of the ventral visual stream, and likely includes feedback from frontal or executive attention systems, as others have suggested (Just & Keller, 2013; Koshino et al., 2008).

These findings, together with the DS/ASD difference that emerged on the OMEFA task, show that attenuated top-down influences of object memories on perception are specific to DS and not ASD. For individuals with DS, an impaired ability to quickly access past experience to guide behavior could have implications not only for perception, but also for adaptive skills in general. A disconnect between fast processes linking memory with perception may not only affect the way we perceive and explain the world (Boucher, Mayes, & Bigham, 2012), it may also prevent the rapid anticipation, imagination, and prediction of future events (Alink, Schwiedrzik, Kohler, Singer, & Muckli, 2010; Rao & Ballard, 1999; Suddendorf, 2010). Future work should determine the significance of this difference in DS for everyday functioning.

### Author Contributions

G. Spanò, J. O. Edgin, and M. A. Peterson contributed to the study design. Testing, data collection and analysis were performed by G. Spanò. G. Spanò performed the interpretation of the data under the supervision of J. O. Edgin and M. A. Peterson. G. Spanò and J. O. Edgin drafted the article and M. A. Peterson provided revisions. L. Nadel provided helpful comments for the interpretation of the results and in drafting of the article findings. C. Rhoads administered the Autism Diagnostic Observation Schedule (ADOS-2). All authors approved the final version of the article for submission.

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### Notes

1. The child version of the OMEFA task was developed by Daphne M. Maurer, Terri L. Lewis, and Michael Slugocki in collaboration with Mary A. Peterson.
2. Those objects they erred on were removed from the OMEFA results discussed previously.
3. We ran a subsequent analysis with participants matched on gender, generating the same pattern of results on the main outcome variables.
4. The OMEFA results presented previously were corrected for the few errors on this task.

### References

- Alink, A., Schwiedrzik, C. M., Kohler, A., Singer, W., & Muckli, L. (2010). Stimulus predictability reduces responses in primary visual cortex. *Journal of Neuroscience*, *30*, 2960–2966. doi:10.1523/JNEUROSCI.3730-10.2010
- American Psychiatric Association. (2013). *Diagnostic and statistical manual of mental disorders* (5th ed.). Washington, DC: Author.
- Anderson, J. S., Nielsen, J. A., Ferguson, M. A., Burbach, M. C., Cox, E. T., Dai, L., . . . Korenberg, J. R. (2013). Abnormal brain synchrony in Down syndrome. *NeuroImage*, *24*, 703–715. doi:10.1016/j.neuroimage.2013.05.006
- Barense, M. D., Ngo, J. K., Hung, L. H., & Peterson, M. A. (2012). Interactions of memory and perception in amnesia: The figure-ground perspective. *Cerebral Cortex*, *22*, 2680–2691. doi:10.1093/cercor/bhr347
- Behrmann, M., Peterson, M. A., Suzuki, S., & Moscovitch, M. (2006). Independent representation of parts and the relations between them: Evidence from integrative agnosia. *Journal of Experimental Psychology: Human Perception and Performance*, *32*, 1169–1184.
- Boucher, J., Mayes, A., & Bigham, S. (2012). Memory in autistic spectrum disorder. *Psychological Bulletin*, *138*, 458–496. doi:10.1037/a0026869
- Brown, J. H., Johnson, M. H., Paterson, S. J., Gilmore, R., Longhi, E., & Karmiloff-Smith, A. (2003). Spatial representation and attention in toddlers with Williams syndrome and Down syndrome. *Neuropsychologia*, *41*, 1037–1046.

- Centers for Disease Control and Prevention. (2008). *Autism information center*. Retrieved from [www.cdc.gov/ncbddd/autism/](http://www.cdc.gov/ncbddd/autism/)
- Cherkassky, V. L., Kana, R. K., Keller, T. A., & Just, M. A. (2006). Functional connectivity in a baseline resting-state network in autism. *NeuroReport*, *17*, 1687–1690.
- Clark, A. (2013). Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behavioral and Brain Sciences*, *36*, 181–204.
- Cohen, J. (1992). A power primer. *Psychological Bulletin*, *112*, 155–159.
- Craft, E., Schütze, H., Niebur, E., & von der Heydt, R. (2007). A neural model of figure-ground organization. *Journal of Neurophysiology*, *97*, 4310–4326. doi:10.1152/jn.00203.2007
- Di Martino, A., Kelly, C., Grzadzinski, R., Zuo, X. N., Mennes, M., Mairena, M. A., . . . Milham, M. P. (2011). Aberrant striatal functional connectivity in children with autism. *Biological Psychiatry*, *69*, 847–856.
- Edgin, J. O. (2013). Cognition in Down syndrome: A developmental cognitive neuroscience perspective. *Wiley Interdisciplinary Reviews: Cognitive Science*, *4*, 307–317. doi:10.1002/wcs.1221
- Edgin, J. O., & Pennington, B. F. (2005). Spatial cognition in autism spectrum disorders: Superior, impaired, or just intact? *Journal of Autism and Developmental Disorders*, *35*, 729–745.
- Edgin, J. O., Spanò, G., Kawa, K., & Nadel, L. (2014). Remembering things without context: Development matters. *Child Development*, *85*, 1491–1502.
- Fidler, D., Hepburn, S., & Rogers, S. (2006). Early learning and adaptive behaviour in toddlers with Down syndrome: Evidence for an emerging behavioural phenotype? *Down Syndrome Research and Practice*, *9*(3), 37–44.
- Gerbino, W., & Salmaso, D. (1987). The effect of amodal completion on visual matching. *Acta Psychologica*, *65*, 25–46.
- Golarai, G., Ghahremani, D. G., Whitfield-Gabrieli, S., Reiss, A., Eberhardt, J. L., Gabrieli, J. D., & Grill-Spector, K. (2007). Differential development of high-level visual cortex correlates with category-specific recognition memory. *Nature Neuroscience*, *10*, 512–522.
- Goldreich, D., & Peterson, M. A. (2012). A Bayesian observer replicates convexity context effects in figure-ground perception. *Seeing and Perceiving*, *25*, 365–395.
- Graf, P. (1990). Life-span changes in implicit and explicit memory. *Bulletin of the Psychonomic Society*, *28*, 353–358.
- Graham, K. S., Barense, M. D., & Lee, A. C. (2010). Going beyond LTM in the MTL: A synthesis of neuropsychological and neuroimaging findings on the role of the medial temporal lobe in memory and perception. *Neuropsychologia*, *48*, 831–853.
- Grill-Spector, K., & Kanwisher, N. (2005). Visual recognition: As soon as you know it is there, you know what it is. *Psychological Science*, *16*, 152–160.
- Hadjikhani, N., Joseph, R. M., Snyder, J., Chabris, C. F., Clark, J., Steele, S., . . . Tager-Flusberg, H. (2004). Activation of the fusiform gyrus when individuals with autism spectrum disorder view faces. *NeuroImage*, *22*, 1141–1150.
- Johnson, S. P. (2001). Visual development in human infants: Binding features, surfaces, and objects. *Visual Cognition*, *8*, 565–578.
- Jolicoeur, P. (1988). Mental rotation and the identification of disoriented objects. *Canadian Journal of Psychology*, *42*, 461–478.
- Jou, R. J., Jackowski, A. P., Papademetris, X., Rajeevan, N., Staib, L. H., & Volkmar, F. R. (2011). Diffusion tensor imaging in autism spectrum disorders: Preliminary evidence of abnormal neural connectivity. *Australian and New Zealand Journal of Psychiatry*, *45*, 153–162.
- Just, M. A., Cherkassky, V. L., Keller, T. A., Kana, R. K., & Minshew, N. J. (2007). Functional and anatomical cortical underconnectivity in autism: Evidence from an fMRI study of an executive function task and corpus callosum morphology. *Cerebral Cortex*, *17*, 951–961.
- Just, M. A., Cherkassky, V. L., Keller, T. A., & Minshew, N. J. (2004). Cortical activation and synchronization during sentence comprehension in high-functioning autism: Evidence of underconnectivity. *Brain*, *127*, 1811–1821.
- Just, M. A., & Keller, T. A. (2013). A theory of autism based on frontal-posterior underconnectivity. In M. A. Just & K. A. Pelphrey (Eds.), *Development and brain systems in autism* (pp. 35–64). New York, NY: Psychology Press.
- Kanizsa, G., & Gerbino, W. (1976). Convexity and symmetry in figure-ground organization. In M. Henle (Ed.), *Vision and artifact* (pp. 25–32). New York, NY: Springer.
- Kaufman, A. S., & Kaufman, N. L. (2004). *Kaufmann Brief Intelligence Test*. 2nd ed. New York, NY: Pearson.
- Kennedy, D. P., & Courchesne, E. (2008). Functional abnormalities of the default network during self-and other-reflection in autism. *Social Cognitive and Affective Neuroscience*, *3*, 177–190.
- Keown, C. L., Shih, P., Nair, A., Peterson, N., Mulvey, M. E., & Müller, R. A. (2013). Local functional overconnectivity in posterior brain regions is associated with symptom severity in autism spectrum disorders. *Cell Reports*, *5*, 567–572.
- Koshino, H., Kana, R. K., Keller, T. A., Cherkassky, V. L., Minshew, N. J., & Just, M. A. (2008). fMRI investigation of working memory for faces in autism: Visual coding and underconnectivity with frontal areas. *Cerebral Cortex*, *18*, 289–300.
- Kravitz, D. J., Saleem, K. S., Baker, C. I., Ungerleider, L. G., & Mishkin, M. (2013). The ventral visual pathway: An expanded neural framework for the processing of object quality. *Trends in Cognitive Sciences*, *17*, 26–49.
- Lee, A. C., Yeung, L. K., & Barense, M. D. (2012). The hippocampus and visual perception. *Frontiers in Human Neuroscience*, *6*(91). doi:10.3389/fnhum.2012.00091/abstract
- Lord, C., Rutter, M., DiLavore, P. C., Risi, S., Gotham, K., & Bishop, S. (2012). *Autism Diagnostic Observation Schedule: ADOS-2*. Torrance, CA: Western Psychological Services.
- MacEvoy, S. P., & Epstein, R. A. (2011). Constructing scenes from objects in human occipitotemporal cortex. *Nature*, *14*, 1323–1329. doi:10.1038/nn.2903
- Mitchell, P., Mottron, L., Soulières, I., & Ropar, D. (2010). Susceptibility to the Shepard illusion in participants with

- autism: Reduced top-down influences within perception? *Autism Research*, 3, 113–119.
- Monk, C. S., Peltier, S. J., Wiggins, J. L., Weng, S. J., Carrasco, M., Risi, S., & Lord, C. (2009). Abnormalities of intrinsic functional connectivity in autism spectrum disorders. *NeuroImage*, 47, 764–772.
- Mosse, E. K., & Jarrold, C. (2011). Evidence for preserved novel word learning in Down syndrome suggests multiple routes to vocabulary acquisition. *Journal of Speech, Language, and Hearing Research*, 54, 1137–1152.
- Mottron, L., Dawson, M., Soulières, I., Hubert, B., & Burack, J. (2006). Enhanced perceptual functioning in autism: An update, and eight principles of autistic perception. *Journal of Autism and Developmental Disorders*, 36, 27–43.
- Müller, C. M., & Nussbeck, S. (2008). Do children with autism spectrum disorders prefer to match pictures based on their physical details or their meaning? *Journal of Mental Health Research in Intellectual Disabilities*, 1, 140–155.
- Murray, E. A., & Bussey, T. J. (1999). Perceptual-mnemonic functions of the perirhinal cortex. *Trends in Cognitive Sciences*, 3, 142–151.
- Murray, E. A., Bussey, T. J., & Saksida, L. M. (2007). Visual perception and memory: A new view of medial temporal lobe function in primates and rodents. *Annual Review of Neuroscience*, 30, 99–122. doi:10.1146/annurev.neuro.29.051605.113046
- Murray, S. O., Kersten, D., Olshausen, B. A., Schrater, P., & Woods, D. L. (2002). Shape perception reduces activity in human primary visual cortex. *Proceedings of the National Academy of Sciences USA*, 99, 15164–15169.
- Nadel, L., & Peterson, M. A. (2013). The hippocampus: Part of an interactive posterior representational system spanning perceptual and memorial systems. *Journal of Experimental Psychology: General*, 142, 1242–1254. doi:10.1037/a0033690
- Nakayama, K., Shimojo, S., & Silverman, G. H. (1989). Stereoscopic depth: Its relation to image segmentation, grouping and the recognition of occluded objects. *Perception*, 18, 55–68.
- Navon, D. (2011). The effect of recognizability on figure-ground processing: Does it affect parsing or only figure selection? *Quarterly Journal of Experimental Psychology*, 64, 608–624. doi:10.1080/17470218.2010.516834
- Needham, A., & Baillargeon, R. (1997). Object segregation in 8-month-old infants. *Cognition*, 62, 121–149.
- Noonan, S. K., Haist, F., & Müller, R. A. (2009). Aberrant functional connectivity in autism: Evidence from low-frequency BOLD signal fluctuations. *Brain research*, 1262, 48–63.
- Panichello, M. F., Cheung, O. S., & Bar, M. (2012). Predictive feedback and conscious visual experience. *Frontiers in Psychology*, 3, 620.
- Pasupathy, A., & Connor, C. E. (1999). Responses to contour features in macaque area V4. *Journal of Neurophysiology*, 82, 2490–2502.
- Pellicano, E., & Burr, D. (2012). When the world becomes too real: A Bayesian explanation of autistic perception. *Trends in Cognitive Sciences*, 16, 504–510.
- Pennington, B. F., Moon, J., Edgin, J., Stedron, J., & Nadel, L. (2003). The neuropsychology of Down syndrome: Evidence for hippocampal dysfunction. *Child Development*, 74, 75–93.
- Perez, L. A., Peynircioğlu, Z. F., & Blaxton, T. A. (1998). Developmental differences in implicit and explicit memory performance. *Journal of Experimental Child Psychology*, 70, 167–185.
- Perrett, D. L., Oram, M. W., & Ashbridge, E. (1998). Evidence accumulation in cell populations responsive to faces: An account of generalisation of recognition without mental transformations. *Cognition*, 67, 111–145.
- Peterson, M. A. (1994). Object recognition processes can and do operate before figure-ground organization. *Current Directions in Psychological Science*, 3, 105–111.
- Peterson, M. A. (2003). Overlapping partial configurations in object memory: An alternative solution to classic problems in perception and recognition. In M. A. Peterson & G. Rhodes (Eds.), *Perception of faces, objects, and scenes: Analytic and holistic processes* (pp. 269–294). New York, NY: Oxford University Press.
- Peterson, M. A. (2012). Plasticity, competition, and task effects in object perception. In J. Wolfe & L. Robertson (Eds.), *From perception to consciousness* (pp. 253–262). New York, NY: Oxford University Press.
- Peterson, M. A., Cacciamani, L., Barense, M. D., & Scalf, P. E. (2012). The perirhinal cortex modulates V2 activity in response to the agreement between part familiarity and configuration familiarity. *Hippocampus*, 22, 1965–1977.
- Peterson, M. A., de Gelder, B., Rapcsak, S. Z., Gerhardstein, P. C., & Bachoud-Lévi, A.-C. (2000). Object memory effects on figure assignment: Conscious object recognition is not necessary or sufficient. *Vision Research*, 40, 1549–1567.
- Peterson, M. A., Gerhardstein, P. C., Mennemeier, M., & Rapcsak, S. Z. (1998). Object-centered attentional biases and object recognition contributions to scene segmentation in left- and right-hemisphere-damaged patients. *Psychobiology*, 26, 357–370.
- Peterson, M. A., & Gibson, B. S. (1994a). Must figure-ground organization precede object recognition? An assumption in peril. *Psychological Science*, 5, 253–259.
- Peterson, M. A., & Gibson, B. S. (1994b). Object recognition contributions to figure-ground organization: Operations on outlines and subjective contours. *Perception & Psychophysics*, 56, 551–564.
- Peterson, M. A., Harvey, E. M., & Weidenbacher, H. J. (1991). Shape recognition contributions to figure-ground reversal: Which route counts? *Journal of Experimental Psychology: Human Perception and Performance*, 17, 1075–1089.
- Peterson, M. A., & Lampignano, D. W. (2003). Implicit memory for novel figure-ground displays includes a history of cross-border competition. *Journal of Experimental Psychology: Human Perception and Performance*, 29, 808–822. doi:10.1037/0096-1523.29.4.808
- Peterson, M. A., & Salvagio, E. (2008). Inhibitory competition in figure-ground perception: Context and convexity. *Journal of Vision*, 8(16), 4–4. doi:10.1167/8.16.4
- Peterson, M. A., & Skow, E. (2008). Inhibitory competition between shape properties in figure-ground perception. *Journal of Experimental Psychology: Human Perception and Performance*, 34, 251–267. doi:10.1037/0096-1523.34.2.251
- Quinn, P. C., & Schyns, P. G. (2003). What goes up may come down: Perceptual process and knowledge access in the

- organization of complex visual patterns by young infants. *Cognitive Science*, 27, 923–935.
- Rao, R. P., & Ballard, D. H. (1999). Predictive coding in the visual cortex: A functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience*, 2, 79–87.
- Renner, P., Klinger, L. G., & Klinger, M. R. (2000). Implicit and explicit memory in autism: Is autism an amnesic disorder? *Journal of Autism and Developmental Disorders*, 30, 3–14.
- Rensink, R. A., & Enns, J. T. (1998). Early completion of occluded objects. *Vision Research*, 38, 2489–2505.
- Ropar, D., & Mitchell, P. (2002). Shape constancy in autism: The role of prior knowledge and perspective cues. *Journal of Child Psychology and Psychiatry*, 43, 647–653.
- Rovee-Collier, C. (1997). Dissociations in infant memory: Rethinking the development of implicit and explicit memory. *Psychological Review*, 104, 467–498.
- Sanguinetti, J. L., Allen, J. J. B., & Peterson, M. A. (2014). A repetition paradigm with figure-ground stimuli reveals that both semantic and shape representations can be accessed outside of awareness. *Psychological Science*, 25, 256–264.
- Sanguinetti, J. L., Trujillo, L. T., Schnyer, D. M., Allen, J. J., & Peterson, M. A. (2014). Increased alpha band activity indexes inhibitory competition across a border during figure assignment. *Journal of Vision*, 14(10), 49–49.
- Stokes, M. G., Atherton, K., Patai, E. Z., & Nobre, A. C. (2012). Long-term memory prepares neural activity for perception. *Proceedings of the National Academy of Sciences USA*, 109, E360–E367.
- Suddendorf, T. (2010). Linking yesterday and tomorrow: Preschoolers' ability to report temporally displaced events. *British Journal of Developmental Psychology*, 28, 491–498.
- Supekar, K., Uddin, L. Q., Khouzam, A., Phillips, J., Gaillard, W. D., Kenworthy, L. E., . . . Menon, V. (2013). Brain hyper-connectivity in children with autism and its links to social deficits. *Cell Reports*, 5, 738–747.
- Tarr, M. J., & Pinker, S. (1989). Mental rotation and orientation dependence in shape recognition. *Cognitive Psychology*, 5, 233–282.
- Trujillo, L., Allen, J., Schnyer, D., & Peterson, M. A. (2010). Neurophysiological evidence for the influence of past experience on figure-ground perception. *Journal of Vision*, 10, 1–21.
- Uddin, L. Q. (2015). Idiosyncratic connectivity in autism: developmental and anatomical considerations. *Trends in Neurosciences*, 38, 261–263. doi:10.1016/j.tins.2015.03.004
- Vecera, S. P., & Farah, M. J. (1997). Is visual image segmentation a bottom-up or an interactive process? *Perception & Psychophysics*, 59, 1280–1296.
- Weng, S. J., Wiggins, J. L., Peltier, S. J., Carrasco, M., Risi, S., Lord, C., & Monk, C. S. (2010). Alterations of resting state functional connectivity in the default network in adolescents with autism spectrum disorders. *Brain Research*, 1313, 202–214.
- Zhou, H., Friedman, H. S., & von der Heydt, R. (2000). Coding of border ownership in monkey visual cortex. *Journal of Neuroscience*, 20, 6594–6611.