Object processing in the infant: lessons from neuroscience

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Object identification is a fundamental cognitive capacity that forms the basis for complex thought and behavior. The adult cortex is organized into functionally distinct visual object-processing pathways that mediate this ability. Insights into the origin of these pathways have begun to emerge through the use of neuroimaging techniques with infant populations. The outcome of this work supports the view that, from the early days of life, object-processing pathways are organized in a way that resembles that of the adult. At the same time, theoretically important changes in patterns of cortical activation are observed during the first year. These findings lead to a new understanding of the cognitive and neural architecture in infants that supports their emerging objectprocessing capacities.

A developmental neuroscience approach to object individuation

We live in a dynamic visual environment in which perceptual contact with objects is frequently lost and then regained. One of our most basic cognitive capacities is the ability to track the identity of objects - to form coherent representations of objects that persist in the absence of direct perceptual experience. The outcome of this process, referred to as object individuation, determines how we think about and act on those objects. The study of how the mature mind solves the individuation problem has a long history in the psychological sciences [1,2], and over the past 20 years developmental scientists have made substantial progress towards understanding the nature and development of object individuation in the infant. To illustrate, researchers have identified developmental hierarchies in the type of information to which infants are most likely to attend when tracking objects through occlusion, age-related changes in the way that individuals are represented, and mechanisms for change [3–6]. Slower to emerge has been an understanding of the cognitive and neural architecture that supports and facilitates this emerging capacity. Such findings could significantly enhance our conceptual models of object identification and representation.

One context in which we can make progress towards this goal is to study the functional organization of the immature brain. Neuroimaging techniques, such as

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functional near-infrared spectroscopy (fNIRS) (Box 1), allow us to localize neural responses and identify the extent to which these responses are stimuli specific (7-9) for review). With a good experimental design we can identify the cortical structures, or a network of cortical structures, that mediate select processes. This can inform developmental theory in several ways. For example, from these data we can gain insight into the functional organization of knowledge from the early days of life before extensive social and educational experiences. We can also identify the effect of naturally occurring differences in early experience (influenced by biological and environmental factors) [10,11] or of specific training procedures [12,13] on brain and behavior. Neuroimaging data can also provide insight into infants' understanding of their world that may not be otherwise evident. Given the limited behavioral repertoire of infants, sometimes it can be difficult to ascertain, from behavioral data alone, the engagement of distinct perceptual or cognitive processes. Patterns of cortical activation can shed light on the extent to which two different stimuli engage common processes, or on conditions under which the same stimulus engages distinct processes. Of course, care must be taken in data interpretation. Because fNIRS measures only from cortical areas, we do not have information about activation in sub-cortical areas that might be part of a processing circuit. In addition, reverse inferences (e.g., inferring from activation patterns that specific processes were engaged) should be drawn with caution [14,15].

Object processing in the adult brain

During the past 15–20 years we have learned a great deal about the functional organization of visual object-processing networks in the adult brain (Figure 1). For example, we know that areas in the primary visual cortex respond to specific features, such as lines, orientation, or color [16–18], whereas areas in the occipito-temporal cortex integrate these features and code objects as wholes, independently of visual perspective [19-22]. Moving posterior to anterior in the temporal cortex, object representations become more abstract. Most relevant to this review is that posterior areas of the temporal cortex mediate processing of objects without reference to type or function, whereas anterior areas are important to higher-level object processing, such as object identification, categorization, and semantic information [23–25]. Although much of this work has focused on bottom-up processes underlying object perception and cognition, there are also top-down processes at work [26,27].

In addition, ventral and dorsal areas make unique contributions to object processing. For example, areas in



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Box 1. Functional near-infrared spectroscopy (fNIRS): a tutorial

The rationale underlying fNIRS is that cortical activation leads to an increase in blood flow and blood volume; the relative changes in amounts of oxygenated and deoxygenated blood delivered to activated areas are assessed by the amount of refracted near-infrared light. Briefly, near-infrared light is projected through the scalp and skull into the brain, and the intensity of diffusely refracted light is recorded. Oxyhemoglobin (HbO) is more sensitive to near-infrared light at ~830 nm, and deoxyhemoglobin (HbR) to that at ~690 nm. Light-intensity modulation during stimulus presentation is compared to that during a baseline event in which no (or a control) stimulus is presented. Change relative to baseline provides information about the hemodynamic response to brain activation. Typically, during cortical activation local concentrations of HbO increase and HbR decrease. A linear relationship between hemodynamics and neural activity [90], and results consistent with other imaging techniques [91,92], provide converging evidence that fNIRS offers a reliable measure of brain function

The use of fNIRS has several advantages over fMRI. fNIRS has much better temporal resolution and can be implemented with awake, engaged infants; typically, fMRI studies are conducted with sleeping or sedated infants to avoid motion artifacts. In addition, fNIRS is

the occipito-temporal region, such as the lateral occipital complex (LOC), mediate shape representations formed on the basis of static contour cues, whereas areas in the posterior parietal cortex, such as the angular gyrus, mediate shape representations formed on the basis of motioncarried information [28–30]. Typically, dorsal areas are important for processing information about the spatiotemporal properties of objects, whereas ventral areas are important for processing information about the featural properties of objects. However, there is evidence that these two pathways interact [31], in addition to ongoing debate about the extent to which the functional distinction between these two pathways is better characterized as 'what' versus 'how', or 'what' versus 'where' [31–33]. non-invasive and safe to use repeatedly and for extended periods of time. Finally, fNIRS technology is cost-effective, portable, and straightforward to use. This makes it accessible and adaptable to a variety of settings. The main advantage of fNIRS over electrophysiological techniques is that hemodynamic responses are localized within 1-2 cm of the area activated, allowing more-accurate identification of the areas from which cortical responses were obtained, fNIRS does have some limitations. First, near-infrared light diffuses rapidly when entering neural tissue, rendering fNIRS unsuitable for the investigation of structures deeper than about 1 cm below the surface of the brain. Second, fNIRS measures neural activation from the head surface without anatomical information about the brain area being studied. There are several ways to resolve this problem [93]. One common approach is to position probes using the International 10-20 system for electroencephalography (EEG) recording and to employ cranio-cerebral correspondences to localize activation [94,95]. Finally, although the spatial resolution of fNIRS is better than that of event-related potential (ERP)/EEG, it is inferior to that of fMRI.

More detailed descriptions of technology, methods, and experimental contexts in which infants have been tested can be found in current reviews [7,8,96–98].

In summary, the adult cortex possesses functionally distinct, hierarchically-organized, parallel object-processing pathways. At the same time, these pathways interact, and top-down as well as bottom-up processes contribute to object recognition and identification. To what extent is the immature cortex similarly organized, and does it operate in a similar fashion?

Object processing in the infant brain

With the introduction of fNIRS into the developmental sciences we now have a tool with which to investigate functional organization of object-processing areas in the human infant. Much of this work has focused on identification of the neural architecture that supports the emerging



Figure 1. Lateral view of the adult human brain with major sulci labeled. Dorsal and ventral streams are indicated with blue and yellow highlighted arrows, respectively. The approximate locations of anterior temporal cortex, posterior temporal cortex, lateral occipital complex (LOC), and posterior parietal cortex are indicated.

capacity of information to use featural information to individuate objects. We first review behavioral findings and then studies that provide insight into the cortical mechanisms that underlie and support behavior.

From the early months of life infants draw on spatiotemporal information as the basis for individuating objects. For example, infants as young 3.5 months show sensitivity to discontinuities in speed and path of motion. and this remains robust throughout infancy [34–37]. These findings are consistent with most models of object processing, which highlight the importance of motion-carried information to infants' apprehension of objects. More controversial were initial claims about the extent to which infants use featural information to individuate objects: some researchers reported that infants do not show sensitivity to object features until late in the first year [37], whereas others reported individuation-by-feature much earlier [38]. Subsequent research revealed that discrepancies in initial findings reflect, in part, the use of tasks with different processing demands; most researchers now agree that young infants can individuate by feature. At the same time, infants are not equally sensitive to all featural information, favoring form over surface features [39]. For example, when viewing shape-difference and color-difference occlusion sequences such as those depicted in Figure 2A, infants aged 4.5 months use the shape difference to individuate objects, but it is not until about 11.5 months that they use a color difference. A similar developmental hierarchy has been observed in object segregation and identification tasks [40,41].

Although visual maturation may play some role in this developmental hierarchy (i.e., the immature visual system has better access to form than color information), it cannot be the whole story: infants perceive color differences long before they use them as the basis for individuating objects. More likely, this developmental hierarchy reflects, to a large extent, both the way the physical world is structured and infants' experience of the physical world, which leads them to perceive form features as being intimately tied to objects and stable over time [39]. By contrast, object color is perceived as arbitrary (e.g., the color of an object does not predict its function or how it will move and interact in the physical world) and unstable (e.g., the perception of color can change over viewing conditions). It is therefore not surprising that differential sensitivity to form versus surface features has been observed in other cognitive tasks that require attention to, and reasoning about, object shape and color [42-45]. The hypothesis that the attention of infants to color is determined, in part, by the way in which the physical world is structured, and by their experience of the physical world, has been supported by studies revealing that, if given experiences that point to the predictive value of color



Figure 2. (A) The wide-screen shape-difference, color-difference, and control test events used in studies investigating infants' use of featural information to individuate objects [39]. Events were presented live in a puppet-stage apparatus. Figures depict one cycle of the event; infants typically saw multiple cycles during each test trial. Infants aged 4.5–12.5 months interpret the shape-difference, but not control, event as involving two objects. It is not until 11.5 months that infants interpret the color-difference event as involving two objects. (B) The location of the nine measurement channels in the fNIRS studies, placed relative to 10-20 coordinates on a schematic of an infant's head. Cranio-cerebral maps ([94], also see [95]) suggest that channels 1 to 3 fall in the anterior temporal cortex, channels 4 and 5 in the posterior temporal cortex, channels 8 and 9 in the occipital cortex. (C) An infant participating in an fNIRS study.

information, or that highlight color as a stable and integral part of an object, infants will then attend to color differences [46–48].

To identify the neural basis of infants' emerging capacity for individuation-by-feature, a series of fNIRS studies were conducted with infants between 3 and 12 months of age [49–51]. Infants viewed shape-difference, color-difference, or control events similar to those used in previous behavioral studies (Figure 2A). Hemodynamic responses to the events were assessed in nine channels located across left occipital, parietal, and temporal cortex (Figure 2B). These studies revealed consistent, robust activation in the occipital cortex to all three events at all ages tested between 4 and 12 months. Other studies, using a slightly different procedure, also revealed activation in the occipital cortex [52–54]. Of greater interest here are patterns of activation observed in the anterior and posterior temporal cortex (ventral areas) and the posterior parietal cortex (dorsal area).

Anterior temporal cortex

On the basis of adult findings, one would expect a different pattern of cortical activation, particularly in anterior temporal areas, to events that engage (rather than fail to engage) the individuation process. That is, behavioral responses should be reflected in patterns of cortical activation. Indeed, across studies, activation was obtained in the anterior temporal cortex only in response to events which infants individuate by feature [13,49–51]. For example, infants aged 3-9 months, who use shape but not color information to individuate objects [39], show anterior temporal activation when viewing the shape-difference but not the color-difference or control event. By contrast, infants aged 11-12 months, who use shape and color information to individuate objects [39,46], show activation in the anterior temporal cortex when viewing either the shape-difference or the color-difference event, but not the control event. This pattern of results was observed in several studies and the findings were robust.

The fact that anterior temporal activation is observed only when infants interpret featural differences as signaling the presence of a distinct object implicates the anterior temporal cortex as central to the individuation process. Two lines of evidence support this interpretation. One line of evidence comes from studies investigating cortical responses to occlusion sequences that involve spatiotemporal discontinuities. Recall that, from an early age, infants draw on spatiotemporal information as the basis for individuating objects. fNIRS studies have revealed that activation is obtained in the anterior temporal cortex to events in which spatiotemporal discontinuities (e.g., discontinuities in path or speed of motion) signal the presence of distinct objects. Control events (such as that in Figure 2A) do not elicit activation in the anterior temporal cortex [49,51]. This confirms and extends the individuation-by-feature results by revealing that the anterior temporal cortex is activated regardless of how the objects were individuated (e.g., on the basis of featural or spatiotemporal information).

The second line of evidence comes from color-priming studies. Behavioral studies have demonstrated that infants younger than 11.5 months, who do not spontaneously attend to color information in object-individuation tasks, can be primed to individuate by color if first shown pretest events that highlight the functional significance of color features [47,55] (Figure I in Box 2). These studies are part of a larger body of work demonstrating that select experiences can alter the type of information to which infants attend when reasoning about physical objects [56–59]. Subsequent fNIRS studies, using this priming procedure (Box 2), investigated whether changes in behavior are accompanied by changes in brain activation. If infants younger than 11.5 months can be primed to attend to color differences in a subsequent objectindividuation task, and individuation-by-feature has a unique cortical signature, we would expect infants who are primed to show that cortical signature. The results of the priming study conducted with infants aged 8 and 9 months were clear: infants who viewed pretest events that highlighted the functional significance of color features individuated by color, and showed activation in the anterior temporal cortex during a subsequent objectindividuation task. Infants who viewed pretest events that do not induce color priming, and infants who viewed no pretest events, did not individuate by color, nor show activation in the anterior temporal cortex [13]. Hence, behavioral and hemodynamic responses were conditionspecific and internally consistent.

Collectively, this research makes clear the importance of the anterior temporal cortex to the individuation process: when the individuation process is engaged and infants infer the presence of two objects, the anterior temporal region is activated. What is currently underspecified is how these objects are represented, which is central to debates about the nature of early object representations [3,4,60]. For example, to what extent are these objects represented as two distinct individuals (object X and object Y) rather than a set of two, and to what extent is featural information included in these representations?

Posterior temporal cortex

The pattern of activation observed in the posterior temporal cortex differs considerably from that observed in the anterior temporal cortex. Most notably, activation patterns appear to be age-related, independently of event. For example, infants aged 3-6 months show activation in posterior temporal areas in response to all three test events displayed in Figure 2A, and the magnitude of the response does not vary by event condition [49,50]. Other research has demonstrated that activation in the posterior temporal cortex is specific to objects, and not to non-object visual stimuli such as faces or reversing checkerboard patterns [61–64]. Furthermore, activation is independent of the properties of the objects involved [49,63]. Collectively, these studies implicate the posterior temporal cortex as a mid-level object-processing area that, although it responds selectively to objects, may be limited in the information associated with those objects. However, posterior temporal responses change markedly during the first year. Regardless of event condition, by 7 months activation in posterior temporal areas wanes, and by 12 months is no longer observed for this task [50,51]. These results suggest that functional reorganization of the ventral objectprocessing network takes place during the second half of

Box 2. Priming infants to attend to color information

A series of studies [47,55] assessed the extent to which the sensitivity of infants to color information could be enhanced by making color functionally relevant. Infants were presented with events before an individuation task in which the color of an object predicted the function in which it would engage. For example, in one experiment, infants aged 9.5 months saw pretest events identical to those depicted in Figure I. After viewing the pound-pour pretest infants, the 9.5month-olds individuated by color in a subsequent different-color (green ball-red ball) test event. Additional research extended this finding to other functions (e.g., stir-lift) and revealed two constraints on the effectiveness of this priming procedure [55]. First, the actions in which the objects engage must be functionally relevant. For example, if the green and red containers perform distinct actions, but these actions do not have an obvious function (e.g., move up and down next to the nail-box, or side to side next to the salt-box, but do not scoop or pour salt), color priming is not observed. This suggests that infants

distinguish between actions on objects that are functionally relevant and those that are not, and weigh these two types of information differently. It is the process of identifying color as relevant to function, an object property to which infants are already sensitive, that facilitates greater attention to color in the subsequent test event. Second, infants aged 9.5 months need to see at least two pairs of pound-pour events with two different object pairs. Seeing two pairs of pound-pour events with the same object pair does not lead to color priming (younger infants aged 7.5 months need to see three different pairs of pound-pour events with three different object pairs). For infants to extract the rule that green objects function differently than red objects, they must see multiple pairs of red and green objects (i.e., multiple exemplar pairs) performing distinct functions. Together, these results suggest that it is the formation of categorical event representations, in which color is linked to object function, that leads to increased sensitivity to color differences in a subsequent test event.



Figure I. The function pound (top row) and pour (bottom row) pretest events of [47]; also used in [13]. The pound and pour events were seen on alternating trials. Infants saw two pairs of pound-pour events, each with a different pair of green and red objects.

the first year. One possibility is that this reflects a paring down of the ventral object-processing pathway. Early in infancy multiple cortical structures, or pathways, may be involved in mid-level visual object processing, some of which become pruned from the network. There are two lines of evidence that support functional pruning of ventral areas. First, areas in the lateral occipital cortex become more selective in their response to visual stimuli between 2 and 3 months of age; whereas object-related responses are widely distributed at 2 months, they become localized to posterior areas of the lateral occipital cortex by 3 months [50,51]. Second, there is evidence from nonhuman primate studies that the neural pathway crucial for visual objectrecognition memory, which projects from the inferior temporal cortex to medial temporal lobe structures, has an abundance of connections early in infancy. By adulthood, some connections are eliminated entirely or become more refined in their distribution [65,66]. These two examples, although drawn from cortical areas that mediate other object-processing functions in the ventral pathway, provide evidence for the importance of functional pruning during infancy. There are several mechanisms by which this pruning could occur, including intrinsic neurobiological factors, early experience of the external environment, and self-organizing principles that lead to select patterns of connectivity within and between cortical areas [67–70].

Insight into the nature of the pruning process can be found in color-priming studies described earlier. Recall that infants aged 8–9 months who see pretest events that highlight the functional significance of color features, but not those who see other pretest events (e.g., events in which different-colored objects undergo actions that are not functionally relevant), demonstrate individuation-bycolor and show activation in the anterior temporal cortex in a subsequent test event. However, infants with both types of experiences show increased activation in the posterior temporal cortex during the subsequent test event [13]. Drawing the attention of the infants to color features, even when the experience is not sufficient to induce individuation-by-color, leads to increased activation in a midlevel object-processing area that is not typically observed in this age group. This suggests that the paring-down process is not complete by 8–9 months, allowing activation of a less frequently used pathway under some conditions.

Parietal cortex

Another intriguing finding revealed by fNIRS is that of age-related changes in parietal cortex activation in response to the shape-difference event [50,51]. Infants aged 6 months and younger (but not older) display activation in the posterior parietal cortex during the shape-difference event. Parietal activation is not obtained in response to the color-difference or control event. In the adult, shape processing can activate dorsal areas for several different reasons [28–31,71], and an assimilation of these findings leads us to competing hypotheses. One hypothesis is that younger infants, whose visual acuity is relatively poor [72–74], are more likely to depend on motion-carried than contour information to extract object shape [75,76]. As a result, younger infants are more likely to show activation in dorsal areas during processing of the shape-difference event. This interpretation is consistent with studies reporting significant maturation of visual capacities during the first 6 months of life [76], and with adult fMRI studies showing that posterior parietal areas are activated when motion-carried information defines object shape, but not when shape is extracted from static contour alone [29,30]. Although there is no direct evidence linking visual maturation, shape processing, and parietal activation, there is evidence that analysis of motion-carried information activates this area of the parietal cortex in young infants [49,51].

An alternative hypothesis focuses on age-related changes in the extent to which shape processing is 'embodied'. There is evidence in adults that processing of information about object form is closely linked to possible actions on objects [77], and often elicits parietal activation [32,67,78]. In the developmental sciences there is a substantial body of research demonstrating an intimate link between perception, action, and cognition in the infant (e.g., [79–81]). One theme that runs through much of this work is the importance of coordinated visual and manual exploration of objects on infants' learning about those objects [46,82,83]. On the basis of these findings, one hypothesis is that processing of 3D object form in real space and time, and under conditions in which objects might be accessible for exploration, engages an actionperception circuit, leading to activation in parietal cortex (cf. [84,85]). Shape processing in this context (i.e., viewing objects in a puppet stage apparatus) is more likely to elicit parietal activation in younger than in older infants for any number of reasons (e.g., shape perception and motor planning are more tightly linked in younger infants; older infants are better able to judge whether objects are within reach or can fit in their hand).

Object individuation: beyond features

Although the focus of this review is the neural mechanisms that support the emerging capacity of infants for individuation-by-feature, there is longstanding and growing interest

Box 3. Outstanding questions

- To what extent is object processing in the infant brain hierarchically organized, as is observed in the adult brain? To what extent is object processing in the infant brain influenced by top-down processes?
- What factors best explain parietal activation observed during shape processing in young infants? Under what conditions is parietal activation observed, and what leads to the developmental change observed in the first year?
- What other cortical areas, besides those investigated in current studies, contribute to the visual object-processing network in the infant brain? Are there hemispheric differences in functional activation of object-processing networks?
- What types of experiences, both experimentally induced and naturally occurring, influence infants' object-processing capacities and associated patterns of cortical activation?
- To what extent do dorsal and ventral areas interact during object processing?
- What role does the anterior temporal cortex play in object-file tracking? Does activation in the anterior temporal cortex predict the creation of an index in the object-file system?

in infants' use of kind information as the basis for individuating objects. This work has generated a great deal of debate because of underlying theoretical differences about the extent to which infants, before language acquisition, have the capacity to represent objects on the basis of kind information [37,86-88]. Neuroimaging data have the potential to help to resolve this debate. To illustrate, behavioral studies demonstrate that, early in life, infants are sensitive to ontological distinctions between types of objects (e.g., animate versus inanimate, or inert versus self-propelled) and possess different expectations for the way these objects should move and interact. Behavioral studies have also revealed that infants aged 10-12 months use these distinctions as a way to track the identity of objects [3,86-88]. Neuroimaging data provide tantalizing evidence that this capacity may exist in even younger infants. For example, in infants 4–9 months of age, different patterns of activation are observed in the anterior temporal cortex in response to function versus non-function events, mechanical versus social interactions, and human versus robotic motion [13,58,89]. In addition, electrophysiological studies reveal distinct responses in occipital areas to objects that infants aged 9 months were previously trained to represent as distinct individuals (without type information) as opposed to a type of object (independent of specific features [60]). Collectively, these results suggest that younger infants possess at least some of the neural architecture to support individuation-by-type. Continued research along these lines would shed light on infants' emerging capacity to succeed on object-individuation tasks that, by the nature of the task demands, require access to type information [3]. Outstanding questions are listed in Box 3.

Concluding remarks

Neuroimaging studies using fNIRS have provided insight into the functional organization of visual object-processing areas in the developing brain. This body of work has revealed localized and process-specific patterns of cortical activation during object-individuation tasks. This work has also demonstrated that functional patterns of cortical activation change during the first year of life. Some of these changes may reflect age-related differences in the way that infants process information, whereas others may reflect the paring of visual object-processing pathways. Systematic investigation of the ventral object-processing network is crucial to fully assess the nature and time-course of the changes observed. As the field moves forward, it will be important for researchers to focus on the identification of developmental processes and mechanisms for change. This work is exciting because it moves the field beyond localization of function in the immature brain and addresses fundamental questions about the cognitive and neural architecture that supports the development of human knowledge.

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