Primer

Infant cognition

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Until fairly recently, young infants were thought to be as cognitively incompetent as they were morally innocent. They were epistemological ‘*tabulae rasae*’, helpless ‘bundles of reflexes’ who spent all of their time sleeping, crying and sucking. In the famous words of William James, infants lived in “*one great blooming, buzzing confusion*”.

This way of thinking was first challenged by the Swiss biologist and developmental psychologist Jean Piaget (1896–1980), who was among the first to explicitly characterize cognitive skills as biological adaptations. Piaget noted that babies’ manual explorations of their environment constituted a basic kind of knowledge, and that these sensory-motor skills created the foundation for mature cognition: the infant comes to ‘grasp’ the world epistemologically by initially grasping and manipulating actual physical objects. But though Piaget granted infants more competence than his predecessors, he was still, from a modern perspective, much too conservative and much too focused on action. In Piaget’s account, infants’ understanding should be entirely restricted to what they can sense and act on in the here and now. But it turns out that if we measure infants’ cognitive competencies in ways that are less demanding than grasping and manipulating objects (e.g., by monitoring their visual attention), they demonstrate fundamental knowledge of how the world works at much younger ages.

Infants’ perception and understanding of the physical world
A fundamental prerequisite for understanding the physical world is the recognition of structures and patterns (Figure 1). In his classic experiments of the 1950s and 1960s, Robert Fantz demonstrated that even at two days of age infants can distinguish visual forms. He developed a technique in which babies were shown two different images simultaneously. If infants looked at them for a different amount of time, it suggested that they distinguished them — preferring those stimuli which captured their attention longer. With this simple technique it was established that young infants have a preference for patterned over plain surfaces and especially for face-like stimuli.

Because not all perceptual discriminations are captured by a spontaneous preference for one of two simultaneously presented stimuli (visual preference method), looking-time techniques were subsequently developed that capitalize on the fact that infants attend to what is new rather than familiar. Infants are repeatedly exposed to a stimulus until they lose interest and look away. In the test phase, they are then shown either the familiar stimulus or a novel one (habituation-dishabituation procedure). If infants show renewed interest towards the novel stimulus, it suggests that they recognize it as being different from the previous ones. In the ‘violation-of-expectation paradigm’ infants are not familiarized with any material, but simply shown events that violate their pre-formed expectations about objects and events, which also leads to increased looking times. With these methods, even very young infants have been shown to discriminate among various properties of stimuli such as color, shape and size.

Piaget thought that for infants anything ‘out of sight’ was also ‘out of mind’ — i.e., that an object ceased to exist once it is no longer visible. His critical test for whether infants possessed ‘object permanence’ was if they searched for an object by intentionally pulling away an occluder covering it. However, they acquire the ability to pull away the occluder only at around 8 months of age. Baillargeon and colleagues thus hypothesized that infants should be capable of showing ‘representational thought’ a lot younger if they did not have to demonstrate it through manual actions. In their famous ‘drawbridge study’, infants were familiarized to a screen rotating alternatingly from an upright to a flat position on a table. Following this familiarization phase, they saw a box being placed behind the screen, making it impossible for the screen to keep rotating all the way onto the table. During the test phase, they saw either a possible event — the screen stopped moving at the position where it would hit the box — or an impossible event — the screen rotated down onto the surface of the table. Infants looked reliably longer at the impossible than at the possible event. Contrary to Piaget’s claim, therefore, infants of only

Figure 1. Cognitive testing in human infants.
An infant attending to a physical event in a looking-time experiment. Photo: Anne Henning, University of Saarbruecken.

a few months of age (and before being capable of manual exploration) know that objects exist even when they are not being perceived.

A related question is how infants come to perceive visual objects as cohesive and separate entities. One obvious indicator to an object's boundaries is isolated motion, i.e. if it changes position independently of other objects. In a pioneering study by Spelke and colleagues, 4-month-olds saw two short rods protruding from behind a rectangle, one from the top and one from the bottom (in a straight line). The two rods then either moved in synchrony in the same direction (appearing to move as one) or, in a control condition, did not move at all. As evidenced by different looking times, infants perceived the two moving rods as a single moving object, but they perceived the stationary rods as two separate objects.

Similar experiments establish that young infants have some rudimentary understanding of discrete quantities. In one study, 4.5-month-old infants were presented with two opaque screens with a gap between them. When two identical looking rubber ducks successively appeared from behind the screens without a duck ever traversing the gap between the screens, infants later expected two ducks behind the screens, not one. They thus seemed to understand the importance of continuous motion for object identity. Similar results were obtained in Wynn's studies on numerosity: 5-month-old infants who witnessed a hand placing two objects behind an occluder one after the other later expected two objects (not one) to be located behind the screen. Infants thus track moving appearances in time and space and use this ability to isolate, identify, and even quantify objects.

Baillargeon extended these findings by investigating infants' understanding of various kinds of physical events instantiating basic causal principles. She found that by around 4 months of age, infants expect, for example, non-supported objects to fall on the ground instead of sustaining themselves in mid-air (gravity), or fallen objects to land on top of other solid things instead of passing through them (solidity). In Leslie's classic experiments it was found that 6-month-olds know that physical causality depends on spatio-temporal contact. These and similar studies have shown that infants possess knowledge of such things as object coherence, solidity, contact (an object cannot exert force on another from a distance), the notion that two objects cannot occupy the same place at a given time, and that one object cannot simultaneously be in two different locations.

These findings have had a major impact on the conception of infant cognition. As Carey and Xu put it, "*there is now ample evidence* […] *that infants as young as 2.5 months of age establish representations of individuated objects and track them through time, even when occluded*". In other words, rudimentary forms of an understanding of physics and number are in place from very early on in ontogeny, before much first-hand experience (and no manipulative experience) has taken place. This has led to a renewed popularity of nativist positions such as that proposed by Spelke and Carey, according to which infants come into the world equipped with 'core knowledge' in the domains of space, objects, actions, and number. However, there is also still some skepticism of looking-time studies and resistance to drawing strong conclusions from them, as many factors may influence the length of time infants gaze at a display.

Infants' perception and understanding of the social world

Infants spend most of their time not individually exploring their physical environment but interacting with other agents. Scientists in recent years have thus also explored how infants understand their social world. In 1977, Meltzoff and Moore reported the astonishing finding that neonates, only a couple of days of age, mimic specific facial expressions that an adult displays towards them, such as mouth opening and tongue protrusion. Given that they could see the adult's behavior but not their own (which they only sensed proprioceptively), this represents a case of intermodal integration. This was in itself surprising, but in many ways the most exciting aspects of this finding were its social implications: it suggested that infants had an innate understanding that other persons are 'like me', which constitutes a critical basis for deeper intersubjective understanding later in life.

But newborns mimic only simple facial expressions, not actions that are directed towards external goals. Following the classic work of Gergely, Csibra, and colleagues, Woodward showed that infants as young as 5 months of age understand that other people's manual actions are directed towards specific goals. In these studies, infants were presented with a human hand reaching repeatedly for the same object, e.g., a ball, until they habituated. When the hand later reached for a new object, e.g., a teddy-bear, the infants showed renewed interest, even when the hand's motion path and the object's location were the same as before. They thus perceived the object as the new goal of the reaching hand. Interestingly, they did not react in this way when an inanimate object (a claw) grasped the target. When infants are given extra practice at reaching for and grasping objects themselves they perceive the reaching actions of others as goal-directed even at 3 months of age — providing support at an older age for a similar 'like me' mechanism.

One characteristic of goal-directed actions, differentiating them from mere non-intentional movements, is that they can fail — the actual outcome does not match the intended one. 18-month-olds make this distinction. Thus, in an imitation task in which a demonstrator failed to achieve her goal, infants reproduced her intended result, rather than just copying her behaviors. Likewise, infants selectively imitate actions that are verbally marked as intentional ('There!') but not those that are marked as accidental ('Whoops!'). An even earlier sensitivity for the difference between intended and unintended acts has been found in 9-month-olds using a simpler response measure than imitation. When infants this age were confronted with an adult who seemed *unwilling* to give them an object they wanted, they responded with impatience and frustration, banging their hands on the table or turning away. The children sat much more patiently and waited when the adult seemed *unable* to pass them the desired object.

In trying to discern what exactly a person is doing and why, infants even factor in the specific circumstances under which an adult behaves in a particular way. When an adult in Gergely and colleagues' experiment turned on a light using her head, 14-month-olds imitated this unusual

Box 1.

Comparative cognition in primates.

Humans shared a common ancestor with other great apes (chimpanzees, bonobos, gorillas, and orangutans) from around 6 to 15 million years ago. We should thus expect to see many cognitive skills in common among all great apes, including humans. A number of recent studies have demonstrated that this is indeed the case, but one study found an especially intriguing pattern of similarities and differences between human infants and two of their closest primate relatives: Herrmann and colleagues administered a comprehensive battery of cognitive tests to large numbers of chimpanzees (n = 106) and orangutans (n = 32), and to 2.5-year-old human children (n = 105). The test battery consisted of 16 different nonverbal tasks assessing all kinds of cognitive skills involving both physical and social problems relevant to primates in their natural environment. The finding was that the children and apes had very similar cognitive skills for dealing with the physical world; but the children — old enough to use some language but still years away from reading, counting, or going to school — already had more sophisticated cognitive skills than either ape species for dealing with the social world. Moreover, a factor analysis of individual differences showed that whereas the chimpanzees had only one factor covering various physical and social-cognitive tasks, the children showed distinct, separate factors for physical cognition and social cognition. These results suggest that at the end of the infancy period, children still have their general great-ape skills of physical cognition, but they already have species-unique skills of social cognition for collaborating, communicating, and learning from others in their cultural group.

action when the adult's hands were visibly free so that the use of the head seemed deliberately chosen and thus appeared to be essential to the action. However, when the adult's hands were occupied, infants preferred to use their hands to turn on the light — presumably because they perceived the adult's strange way of accomplishing this as forced upon her by the lack of a more convenient alternative. Infants seem to understand not just what someone is doing, but, in some circumstances, also why they are doing it.

Just as infants know what others do intentionally, they also know what others see. While even infants in the first six months of life turn in the general direction in which another person looks, their gaze-following becomes much more sophisticated and precise around their first birthday. Not only do they follow another's line of view to hidden spaces, they also correctly refrain from following another's head turn when the person's eyes are closed, blindfolded, averted or when her vision is blocked by a barrier — indicating an awareness that open eyes and a clear line of sight are requirements for seeing. This behavior often marks the beginning of an episode of 'joint attention', in which infant and adult share an object of interest with the mutual awareness of it being shared — as evidenced by the 'checking looks' and 'knowing smiles' that infants display towards the adult. Other ways of initiating joint attention are shown by one-year-olds when they point out objects to others declaratively, show others objects by bringing them into the mutual line of sight or follow others' pointing gestures.

The ability to engage in joint attention is foundational for the social-cognitive development of infants, including their language acquisition and later 'theory of mind'. Engaging in joint attention with another person tunes infants in to what their partner 'knows'. In a series of experiments involving an adult ambiguously requesting objects from infants, Moll and colleagues found that one-year-old infants were able to determine which of several objects an adult did or did not know from prior experience, independent of the child's own experience with them. However, this ability of theirs was limited to situations of joint attention: only when the one-year-olds jointly attended to the objects that an adult became familiar with were they later able to distinguish between what was 'old news' versus 'new news' for the adult. Joint attention thus allows infants to come to understand others' knowledge states. Habituation studies suggest that infants at this age may even distinguish true beliefs from false beliefs, and one interactive study suggests something similar. If infants understand false beliefs, this means that they have all of the basic elements of a representational theory of mind with which to predict what others will do not based on reality, but based on what those others believe about reality.

Finally, a recent frontier in the study of infant social cognition is their skills and motivations for cooperation. Warneken and Tomasello found that 18- and 24-month-olds are able to cooperate with adults in various ways. When, as programmed, the adult stopped participating at a certain point during the activity, infants attempted to re-engage him, suggesting that they understood their joint activity as structured by an underlying joint goal, even joint commitment, to the cooperation. Infants of the same age also altruistically help others to achieve their individual goals. Infants in the second year of life were found to help an adult in various scenarios without any direct benefit for themselves; for instance, they spontaneously removed physical obstacles that hindered the adult, and showed him means that they knew were effective to bring about the intended result. One may think that infants must be trained in order to show such laudable behavior, but it has in fact been found that extrinsic rewards undermine rather than promote infants' propensity to help. Moreover, Hamlin and coworkers showed that infants as young as 6 months of age prefer inanimate figures that they see as helpers over those they see as hinderers, and in habituation experiments even 3-month-olds discriminate helpers from hinderers. These results clearly challenge the view that infants start out as egoists who have to be trained to become prosocial through systematic cultural intervention. Rather, they suggest that altruism and cooperation comes to humans naturally from the start.

Evolution and human cognitive development

Interestingly, virtually all of the amazing skills that human infants show in understanding their physical world are also displayed by non-human primates (Box 1). Some infants' skills for understanding their social world are shared with other primates as well, but at the end of the infancy period, at around two years of age, while infants still have almost identical skills as their primate cousins in their understanding of objects, space, causality, and so forth, they are clearly unique in their social-cognitive skills for engaging in social learning, communication, and collaboration with others. These social-cognitive skills represent a species-unique kind of 'cultural intelligence' that enables human children to acquire the skills and knowledge of those around them, and so to amplify their cognitive skills manyfold. Humans' most basic cognitive skills for understanding their physical and social worlds are thus clearly part of their evolutionary heritage, and the teaching, socialization, and language characteristic of human cultures then builds on this foundation to take human cognition to even greater heights.

Further reading

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Multicellular development in a choanoflagellate

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Little is known about how the first animals evolved from their single-celled ancestors. Over 120 years ago, Ernst Haeckel proposed that animals evolved through "*repeated self-division of* [a] *primary cell,*" [1] an idea supported by the observation that all animals develop from a single cell (the zygote) through successive rounds of cell division [2]. Nonetheless, there are multiple alternative hypotheses [3], including the formal possibility that multicellularity in the progenitor of animals occurred through cell aggregation, with embryogenesis by cell division being secondarily derived. The closest known relatives of animals, choanoflagellates, are emerging as a model system for testing specific hypotheses about animal origins [4–6]. Studying colony formation in choanoflagellates may provide a context for reconstructing the evolution of animal multicellularity. Here, we find that the transition from single cells to multicellular colonies in the choanoflagellate *Salpingoeca rosetta* (previously known as *Proterospongia* sp.) occurs by cell division, with sister cells remaining stably attached.

The life cycles of all choanoflagellates feature a prominent single-celled phase, but many species are also capable of forming colonies of morphologically similar cells [7–9]. Phylogenetics and the reconstruction of ancestral character states within the choanoflagellate group indicate that colony formation either evolved before the diversification of two of the three major choanoflagellate clades, or that it evolved independently multiple times [6]. It is also possible that the last common ancestor of animals and choanoflagellates was capable of forming multicellular colonies [6]. Thus, studies of the colony-forming choanoflagellate *S. rosetta* offer an opportunity to test hypotheses about the cell biology of colony formation and its potential relevance to the evolution of animal multicellularity.

S. rosetta can exist as either single cells or rosette-shaped colonies that contain between four and ~50 cells arranged in closely packed spheres (Figure 1A). To determine how colonies form, cultures of solitary *S. rosetta* cells were induced to form colonies by co-cultivation with the prey bacterium *Algoriphagus* sp. and monitored for at least 12 hours by time-lapse microscopy (Supplemental Information). *S. rosetta* colonies were consistently observed to form through cell division and never by aggregation (Figure 1A). Cell division during colony formation was asynchronous, suggesting that the cell cycle is not coordinated between sister cells in colonies (Figure 1B).

Despite these observations, it is formally possible that *S. rosetta* colonies might form by aggregation at low frequency or under conditions that do not favor cell proliferation. In this case, colony formation through aggregation might be observed in cultures in which cell division is blocked. Therefore, we tested whether the cell cycle inhibitor, aphidicolin [10], can block cell proliferation and thus colony formation in *S. rosetta*. In the presence of aphidicolin, *S. rosetta* cells fail to divide, yet continue to increase in size and otherwise appear normal (Figure 1C). Upon removal of the drug, cell division resumes. To test whether colonies can form in the absence of cell division, *S. rosetta* cells were treated with either aphidicolin or DMSO (as a negative control) prior to induction of colony formation (Figure 1D). DMSO-treated cultures developed colonies within 24 hours after induction, while cultures incubated with aphidicolin failed to form colonies, even after 96 hours of induction. Removal of aphidicolin from induced cultures after 36 hours of treatment permitted the development of colonies, demonstrating that the drug's effect was reversible and that the formation of colonies is dependent upon cell proliferation. Taken together, these findings demonstrate that *S. rosetta* colonies form by cell division and not by cell aggregation.

Our finding is consistent with the hypothesis that the last common ancestor of animals and choanoflagellates was capable of simple multicellularity. An important test of this hypothesis will be to determine whether colony