Developmental Psychology: A Precursor of Moral Judgment in Human Infants?

Pierre Jacob, Emmanuel Dupoux

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Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08540, USA.
E-mail: gould@princeton.edu

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Human infants evaluate social interactions well before they can speak, and show a preference for characters that help others over characters that are not cooperative or are hindering.

P. Jacob[1] and E. Dupoux[2,3]

The field of developmental psychology has advanced tremendously over the past thirty years, progress that is well illustrated by the recent paper of Hamlin *et al.* [1]. Pioneering work of Elisabeth Spelke, Susan Carey, Renée Baillargeon, Karen Wynn and many others has shown that, far from being immersed into William James' world of "booming and buzzing confusion", preverbal infants have highly structured expectations about the world: they parse the world into discrete and countable objects with properties like solidity and continuity through space and time [2,3]. Infants further distinguish between inanimate and animate objects: the former are governed by the laws of Cartesian physics; the latter are self-propelled and infants take them to be rational agents of goal-directed behaviors [4,5]. These discoveries have been made possible by two major steps: first, the assumption that cognitive development is based not on general-purpose principles of associative learning, but rather on genetically determined, domain-specific acquisition systems [6–9]; and second, the emergence of astute experimental designs, capable of probing preverbal infants' behavioral reactions in response to their perception of simple *versus* complex, old *versus* new, or possible *versus* impossible, events — providing insight into their perception, memory and expectations [10].

So far, the social and moral world of preverbal infants has remained pretty much *terra incognita*. Past studies by Piaget [11], Kohlberg [12] and others have described human infants as being self-oriented or egocentric, or only responsive to adults' authority. But these studies used either informal and anecdotal observations or verbal reports, which are not readily usable before the age of three years old. Using two nonverbal experimental techniques, Hamlin *et al.* [1] have now shown that infants can evaluate a geometrical, cartoon-like agent involved in either helping or hindering another character who is trying to climb a hill (Figure 1). More specifically, a preference-choice technique shows that 10-month-old and even 6-month-old infants display a preference for the helping agent over the hindering one, and a violation of expectation paradigm shows that the 10-month-olds are
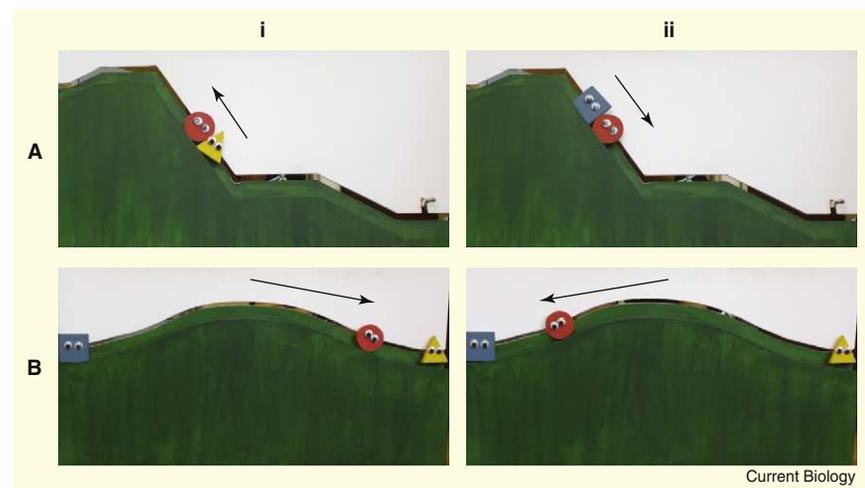

Figure 1. The nonverbal experimental technique used by Hamlin *et al.* [1].
(A) Social interaction events shown to infants. The climber (red character) attempts to climb the hill twice, each time falling back to the bottom of the hill. On the third attempt, the climber is either bumped up the hill by the helper (yellow character, left panel) or bumped down the hill by the hinderer (blue character, right panel). In the violation of expectation task (B), infants' looking times are measured for two events: the climber moves from the top of the hill to sit with the character on the right (left panel) or the left (right panel). In the choice paradigm, infants are presented with two toys, the helper and the hinderer, and are asked to choose one. (Reproduced with permission from [1].)

more surprised to see the climber display a preference for the hinderer over the helper.

These results mesh well with the fast growing evidence that moral and social cognition is based on so-called 'core systems' — computationally specialized systems which process, in an automatic and unconscious fashion, evolutionarily relevant social and emotional information [13]. First, adults make very quick moral judgments, but, as Haidt [14] has shown, they often find themselves utterly dumbfounded when asked for explicit justifications. Secondly, as Blair [15] has argued, individuals who fail to empathize with the emotional distress of others, develop psychopathic behavior and are impaired in moral evaluation. Thirdly, as emphasized by Mikhail [16] and Hauser [17], moral judgments may require the representation of the intentional structure of social interactions, the computation of which is based in turn on deeply unconscious abstract principles. Finally, animal studies provide some evidence for the existence of complex social behaviors such as punishing cheaters [18] and comforting distressed conspecifics [19], which in humans may reflect moral judgments.

Does this mean that preverbal infants entertain moral thoughts? As Hamlin *et al.* [1] rightly put it, their experiment merely demonstrates that 6-month-olds display preferences for agents who help, rather than hinder, some unrelated third-party. Awareness of the work in other domains of cognitive development, however, should make us suspicious of the claim that there is a single cognitive foundation for human moral cognition. Indeed, in the case of numerical cognition, there is not a single preverbal core system for numbers, but at least two: one system for tracking a small number of objects, and another system for evaluating large quantities or amounts of stuff [20]. Note that neither of these systems is genuinely numerical in the sense of number theory. Similarly, one could propose that morality rests not on one, but on several, core systems, none of which is intrinsically moral.

In the situation used by Hamlin *et al.* [1], there are at least two potentially confounded factors. The hindering agent is both frustrating the climber's intention and also potentially harming him by harshly pushing him on the slope. Similarly, if and when the helping agent promotes the climber's goal *after* the hindering agent has performed his negative act, then the question arises whether the helping agent might also provide comfort to the climber. In the abstract of their paper, Hamlin *et al.* [1] tend to confuse two different social contrasts: helping *versus* hindering, and comforting *versus* harming. These two dimensions are dissociable: one can hinder the act of another agent so as to prevent him from harming himself. Conversely, one can help another agent perform a harmful act on himself. In addition, these two dimensions may elicit different emotions: hindering an agent's act causes the agent's anger; harming a patient causes the patient's distress. If so, then there are reasons to think that these two dimensions are processed by two separate systems. Further research is needed to elucidate the number of separate social dimensions that are relevant for human infants.

Before closing, we would like to comment on the developmental difference found by Hamlin *et al.* [1] between the 6-month-old and the 10-month-old infants. They found that the 6-month-olds showed a preference for the helper over the hinderer, but were not more surprised to see the climber approach the hinderer as opposed to the helper. The 10-month-olds reacted in both tasks. The authors imply that there could be a developmental trend whereby infants would first use their own first-personal emotional responses in order to evaluate social interactions involving unrelated parties. Only later do they become able to represent the social evaluation of an agent by another character who was either helped or hindered by the agent's act. We suggest that the lack of emotional cues in the climber's responses to either the helper's positive act or the hinderer's negative act might explain the fact that 6-month-olds failed to display more surprise when they saw the climber join the hindering agent than the helping agent. At least, it is worth testing whether adding emotional cues on the part of the climber might enhance the surprise of 6-month-olds.

In brief, the findings by Hamlin *et al.* [1] raise several fascinating issues: is there a unique capacity for social evaluation or several? What is the link between the ability to evaluate helping vs. hindering agents and culturally acquired moral beliefs and norms regarding social cooperation? Are these systems partly learned on the basis of early social interactions? Or are they genetically pre-wired? Are non-human animals able to discriminate between helping and hindering agents too?

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[1]Institut Jean Nicod, Ecole des Hautes Etudes en Sciences Sociales, Departement d'Etudes Cognitives-Ecole Normale Supérieure, Centre National de la Recherche Scientifique, 29 rue d'Ulm, Paris 75005, France. [2]Laboratoire de Sciences Cognitives et Psycholinguistique,

Ecole des Hautes Etudes en Sciences Sociales, Departement d'Etudes Cognitives-Ecole Normale Supérieure, Centre National de la Recherche Scientifique, 29 rue d'Ulm, Paris 75005, France. [3]Maternité Port-Royal, Faculté de Médecine Port Royal-Cochin, APHP, Université René

Descartes, 123 boulevard de Port-Royal, F75014 Paris, France.
E-mail: emmanuel.dupoux@gmail.com

Plant Immunity: AvrPto Targets the Frontline

Bacterial pathogens must suppress host defences to cause disease. New research shows that the *Pseudomonas* effector protein AvrPto does so by directly targeting plant transmembrane receptor kinases involved in bacterial perception.

Cyril Zipfel and John P. Rathjen

An old saw in plant pathology states that most plants are resistant to most pathogens. An important aspect of this phenomenon is host recognition of immutable pathogen molecules, known as PAMPs (for pathogen-associated molecular patterns), by pattern recognition receptors (PRRs). Only a few plant PRRs are known; the plasma-membrane-localised leucine-rich-repeat receptor kinases (LRR-RK) FLS2 and EFR recognise the bacterial PAMPs flagellin and EF-Tu, or their peptide epitopes flg22 and elf18, respectively [1]. If PAMP recognition is not evaded or suppressed, host immunity is elicited and pathogen growth is halted. Importantly, Zhou and colleagues [2], in a recent issue of *Current Biology*, now show that the bacterial virulence factor AvrPto targets PRRs directly to suppress PAMP recognition in host plants.

Bacterial pathogens secrete a suite of virulence 'effector' proteins through a specialised type III secretion system (TTSS) [3]. The model pathogen, *Pseudomonas syringae* pv *tomato* DC3000 (*Pto* DC3000), secretes more than 30 effectors, and mutants defective in the TTSS machinery ('*ttss*' mutants) are not infectious. However, mutants lacking individual effector genes display subtle or no virulence phenotypes, suggesting that effectors act redundantly or additively. Nevertheless, several effectors have been shown to inhibit or suppress plant immune responses and to contribute to virulence [3,4]. Despite these advances, in most cases the effectors' targets in the plant cell are still unknown,

reflecting our generally poor knowledge of plant immune-signalling pathways.

Plant immunity comprises several layers of recognition of which PAMP-triggered immunity (PTI) is the first. A secondary layer involves recognition of effectors by dedicated resistance (R) proteins. To infect a given host, microbes must either avoid PTI or suppress it through the actions of effectors. In turn, some plants have evolved resistance (R) proteins to detect these effectors, causing effector-triggered immunity (ETI), which is often accompanied by a form of cell death known as the hypersensitive response (HR). The dynamic interplay of these two forms of immunity as the host struggles to recognise elusive pathogens reflects the evolutionary pressures of these intimate relationships [5,6].

The *Pto* DC3000 effector protein AvrPto is a small triple-helix protein that, like several other effectors, is targeted to the plasma membrane by N-myristoylation [7]. Although AvrPto contributes demonstrably to pathogen virulence, it was identified initially by its ability to induce ETI in tomato plants carrying an effector recognition complex composed of the protein kinase Pto and Prf, a canonical R protein of the nucleotide binding-LRR family [6] (Figure 1). AvrPto interacts directly with Pto in tomato cells. However, AvrPto contributes to virulence in tomato lines lacking Pto and/or Prf [8–10]. Strikingly, ectopic overexpression of AvrPto in the plant model *Arabidopsis thaliana* restores growth of a *Pto* DC3000 *ttss* mutant to almost wild-type levels [11], suggesting

that AvrPto suppressed PTI to a sufficient level to allow growth of this strain. Moreover, transgenic expression of AvrPto suppressed the expression of genes encoding defence and secreted cell-wall proteins and also inhibited callose deposition induced by a *Pto* DC3000 *ttss* mutant. AvrPto was therefore proposed to suppress cell-wall-based plant defences. However, several subsequent publications reported that AvrPto seems to work very early in PTI, because AvrPto expression in *Arabidopsis* and *Nicotiana benthamiana* inhibits several early markers of PTI [12–14]. Interestingly, AvrPto expression inhibits early responses induced by several PAMPs [13,14]. Taken together, these results showed that AvrPto must target signalling components directly at, or immediately proximal to, recognition events at the plasma membrane. The major question, however, remained; how does it do it?

Until recently, no biochemical function could be assigned to AvrPto. Recent structural work suggests that AvrPto acts as an inhibitor of Pto by occluding the kinase catalytic cleft [15]. Somewhat confusingly, the kinase-inhibition activity of AvrPto is dispensable for elicitation of Pto–Prf-mediated resistance [15], suggesting that an alternative protein kinase target(s) might underlie the virulence activity of AvrPto. Based on homologies between the kinase domain of Pto and those of FLS2 and EFR, Zhou and colleagues [2] postulated that AvrPto might interact with and inhibit these LRR-RLKs. Indeed, AvrPto interacts with FLS2 and EFR both *in vitro* and *in vivo* when expressed ectopically in plant cells. Furthermore, AvrPto inhibits autophosphorylation of FLS2 and EFR in a dose-dependent manner. Thus, AvrPto is an inhibitor of PRR kinase domains (Figure 1), consistent with its plasma-membrane localisation and variety of suppression activities.