LPS and IL-6 are known stimulators of both CREBH and hepcidin (5, 6). We tested whether CREBH is required for hepcidin response to LPS in vivo by analysis in wild-type and $Crebh^{-/-}$ mice. CREBH deficiency did not impair induction of the hepcidin gene in response to inflammatory challenge, although the increased expression of hepatic hepcidin mRNA was lower in $Crebh^{-/-}$ animals compared to wild-type mice (Fig. 4C). The data suggest that the CREBH-hepcidin axis may cooperate with other well-characterized signaling pathways (such as IL-6/STAT3) to stimulate hepcidin expression during inflammation (fig. S9).

The liver regulates drug detoxification, lipid metabolism, glucose homeostasis, and, as emerged after the discovery of hepcidin, iron homeostasis. As professional secretory cells, the hepatocytes likely face a subtle but persistent condition of ER stress due to the extremely high requirement for protein folding within the ER lumen (21). Homeostasis in the ER is tightly monitored through a series of adaptive programs, called the unfolded protein response (UPR). The UPR not only regulates protein folding capacity within the ER, but also modulates fundamental physiological processes, such as differentiation of specialized cell types and cell metabolism (22). Here, we show that this adaptive program also influences iron metabolism, through activation of hepcidin, the iron hormone. CREBH stable occupancy of the

hepcidin promoter may serve as a "stress sensor" for intracellular or extracellular signals perturbing homeostasis (fig. S9). CREBH may act alone or recruit other stress-related transcription factors, such as XBP1, as shown here. Under conditions of severe ER stress, hepcidin activation and iron withdrawn from the bloodstream may facilitate a general defense mechanism and an innate immune response, in a manner similar to that which occurs during hepcidin activation in response to systemic inflammation (1). Overall, it seems that, at variance with other ER stress–induced factors, CREBH activates the expression of classic acute-phase response genes, such as SAP and CRP (4) and hepcidin (this report), a peptide that also qualifies as a main acute-phase response gene.

The regulation of hepcidin by ER stress links the cellular response involved in protein quality control to innate immunity and iron homeostasis. Apparently, hepcidin "senses" not only extracellular stimuli, such as iron fluctuations, erythroid factors, and cytokines (1), but also stress signals arising intracellularly (fig. S9).

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Capuchin Monkeys Display Affiliation Toward Humans Who Imitate Them

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During social interactions, humans often unconsciously and unintentionally imitate the behaviors of others, which increases rapport, liking, and empathy between interaction partners. This effect is thought to be an evolutionary adaptation that facilitates group living and may be shared with other primate species. Here, we show that capuchin monkeys, a highly social primate species, prefer human imitators over non-imitators in a variety of ways: The monkeys look longer at imitators, spend more time in proximity to imitators, and choose to interact more frequently with imitators in a token exchange task. These results demonstrate that imitation can promote affiliation in nonhuman primates. Behavior matching that leads to prosocial behaviors toward others may have been one of the mechanisms at the basis of altruistic behavioral tendencies in capuchins and in other primates, including humans.

In everyday life, we often unintentionally imitate the body postures, gestures, and mannerisms of our social interaction partners (1), a phenomenon that has been termed the "chameleon effect" (2). This form of imitation, which occurs completely unconsciously, can have profound effects on subsequent social interactions: The imitated person reports increases in shared rapport, liking, and feelings of empathy with the interaction partner (2) and is also more likely to display prosocial behaviors such as helping others, leaving more generous tips, or donating money to charity (3, 4). Imitation therefore increases affiliation, empathy, and

rapport between individuals, and it undoubtedly plays an important role in maintaining harmonious relationships with others (5).

Being able to cultivate successful social relationships is likely to carry substantial adaptive value. Individuals with strong social bonds who receive support from others are thought to have an evolutionary advantage over those who are ostracized from a group (3, 5). Nonconscious imitation may therefore be an evolutionary adaptation that facilitates group living and may occur among other social primate species. Great apes and macaques share with us the capacity to recognize imitation (6–8), but it is presently

unclear whether imitation may also facilitate positive social interactions in nonhuman primates. That is, do other primates show increased levels of affiliation toward an individual who displays behaviors similar to their own? We addressed this question by studying the effects of imitation on the behavior of capuchin monkeys, a highly social and socially tolerant New World primate species. Observational and experimental evidence suggests that capuchins are easily influenced by others' behavior (9–11) and are thus likely to recognize when others display behaviors matching their own actions. Moreover, because capuchins are strongly bonded into social groups, they may share with humans this mechanism to facilitate social group living; namely, increasing affiliation toward those who display matching behaviors. We therefore tested whether capuchins recognize imitation and whether imitation positively affects capuchins' social interactions.

In experiment 1, we investigated whether capuchins differentiate between an experimenter imitating them and an experimenter performing

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contingent actions but not imitating them. Following the established research designs with infants (*12*, *13*), two experimenters, each holding a small plastic ball, faced each monkey (Fig. 1). During the baseline phase, both experimenters performed actions that are commonly performed by capuchins (poking the ball with their fingers, mouthing the ball, and pounding the ball on a surface) (*14*). Analysis of visual preferences showed that monkeys did not discriminate between experimenters [mean, 36.23 s and 40.05 s; $t(10) = -0.81$, $P = 0.44$]. During the manipulation phase, monkeys were given an identical ball. One experimenter imitated the monkeys' ball-directed actions, whereas the other experimenter performed contingent but nonmatching actions (*14*). Monkeys looked longer at the imitator while they were manipulating the ball and hence while they were being imitated by the imitator [$t(10) = 2.23$, $P = 0.050$] (Fig. 2). Thus, capuchins are sensitive to the actions of others that match their own actions, and they prefer to look at imitating individuals.

Proximity to others is a reliable indicator of underlying affiliative relationships in capuchins

and other primates (*15*). In experiment 2, we tested whether capuchins show increased proximity to an imitator rather than a non-imitator. At the start of the experiment, two experimenters faced each monkey for a 1-min period, one standing on the left side and one standing on the right side of a test cage. Monkeys could freely move within the three chambers of the test cage and choose whether to spend time in front of one of the experimenters or in a neutral middle position equidistant between experimenters (Fig. 1). During the first proximity measurement, monkeys spent similar amounts of time in front of both experimenters [41.2 and 36.0% of the trial; $t(9) = 0.65$, $P = 0.53$] (Fig. 3). As in experiment 1, monkeys were then given a small plastic ball, and one experimenter imitated the monkey's ball-directed actions while the other performed temporally contingent but structurally nonmatching actions. Monkeys looked longer at the imitator while manipulating the ball and hence while being imitated [$t(9) = 2.95$, $P = 0.016$] (Fig. 2). After the manipulation phase, imitator and non-imitator switched positions in

front of the test cage, and for 1 min, monkeys could again choose whether to spend time in front of an experimenter or in the middle of the test cage equidistant between experimenters. Monkeys now spent significantly more time in front of the imitator than the non-imitator [mean imitator, 44.0%; mean non-imitator, 27.1% of the trial; $t(9) = 2.29$, $P = 0.048$] (Fig. 3).

One possible explanation for this effect might be that it is not imitation but rather the difference in looking time during the manipulation phase that led to the monkeys having greater familiarity with the imitator and thereby causing the shift in the monkeys' preference for the imitating experimenter. Alternatively, the imitator may have been perceived as being more attentive to the monkeys and therefore may have been preferred in the subsequent proximity test. To test whether attention alone may have caused the observed effect on social preference, in experiment 3 we first conducted a baseline proximity preference as in experiment 2. Two experimenters stood in front of the monkeys, one to the left and one to the right of the test cage, and for 1 min, monkeys could choose to spend time in front of an experimenter or in the middle of the test cage equidistant between experimenters. Monkeys spent similar amounts of time in front of both experimenters [36.9 and 32.0% of the trial; $t(10) = 0.74$, $P = 0.48$] (Fig. 3). Monkeys were then given a small plastic ball, and one experimenter faced and looked at the monkeys, whereas the other experimenter turned around and faced away from the monkeys. Both experimenters remained passive and did not move while the monkeys manipulated the ball. Being sensitive to gaze (*16*), monkeys looked significantly longer at the experimenter facing them during the manipulation phase [$t(10) = 6.41$, $P < 0.001$] (Fig. 2). After the manipulation phase, the two experimenters switched places in front of the test cage, and monkeys could again choose for 1 min whether to spend time in front of one of the experimenters or in the middle of the test cage equidistant between experimenters. Unlike in experiment 2, monkeys now spent similar amounts of time in front of experimenters [mean looking at monkey, 37.8%; mean looking away from monkey, 27.4% of the trial; $t(10) = 1.56$, $P = 0.15$] (Fig. 3). Thus, it appears that it is the process of being imitated rather than simple familiarity that caused monkeys to increase proximity to the imitator in experiment 2.

To investigate whether imitation also affects social interactions, we tested the effects of imitation on monkeys' interactions with an imitator in a token exchange task. A token exchange by its very nature is an interaction between two partners, one providing a token and the other providing a food item (*17*). Several factors may influence a monkey's willingness to exchange tokens with an experimenter; for example, a monkey might refuse to exchange tokens with a person whom they fear [supporting online material (SOM) text]. Therefore, a monkey's emotional reaction toward an experimenter may

Fig. 1. Schematic of experimental setup in experiments 1 through 5. For proximity measures and token exchanges, monkeys had access to cages **A** through **C**. Monkeys were considered to be in proximity to an experimenter when they entered cage A or C. During the manipulation phases (imitation or gaze control), monkeys were restricted to cage B.
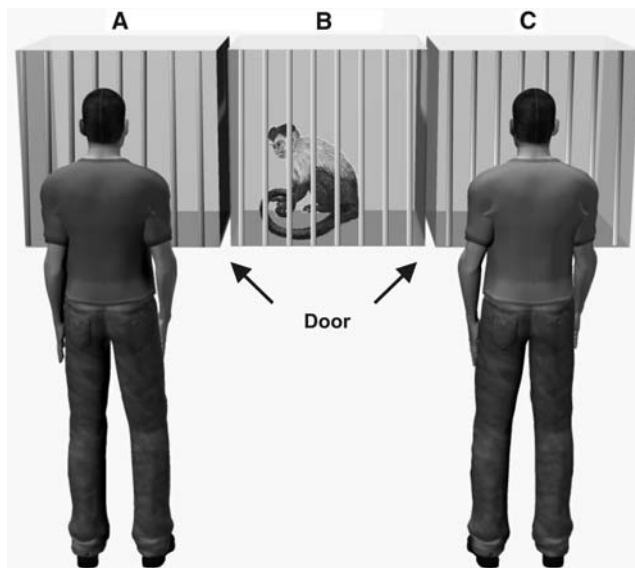
Fig. 2. Average looking time at experimenters while monkeys were manipulating the ball during manipulation phases (imitation or gaze control) in experiments 1 through 5. Gray bars represent the imitator/experimenter facing the monkey; white bars represent the non-imitator/experimenter facing away from the monkey. *$P = 0.05$, **$P < 0.05$, two-tailed t tests [experiments 1 and 3, $n = 11$ monkeys; experiments 2, 4, and 5, $n = 10$ monkeys; see (*14*)]. Error bars represent SEM.
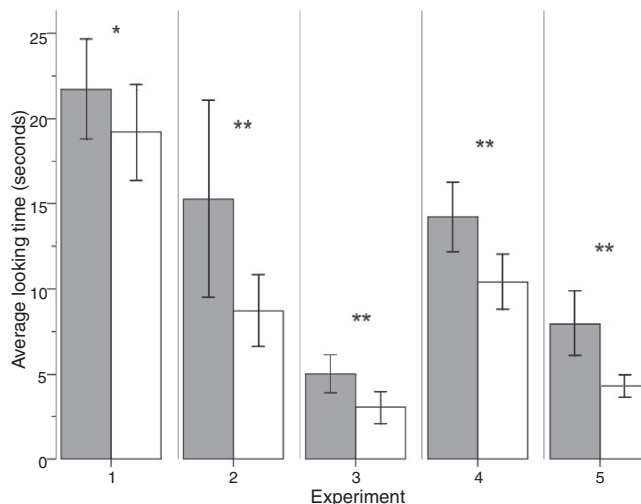
Fig. 3. Average behavioral preferences (proximity and token exchanges) for experimenters in experiments 2 through 5 before and after the manipulation phases (imitation or gaze control). Proximity measures in experiments 2 and 3 were converted into a percentage of the total phase duration. Token exchanges in experiments 4 and 5 were converted into a percentage of total exchanges (10 trials per phase = 100%). The top of the boxes represents the 75th percentile, the bottom of the boxes represents the 25th percentile, and the line in the middle represents the median. Gray boxes represent the imitator/experimenter facing the monkey; white boxes represent the non-imitator/experimenter facing away from the monkey. **$P < 0.05$, two-tailed t tests.
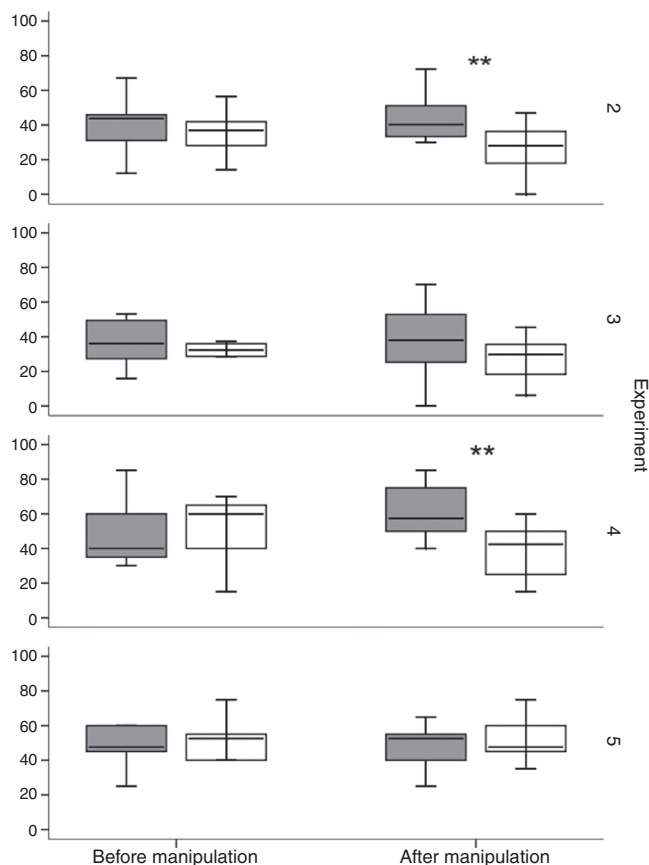
significantly affect a monkey's willingness to exchange tokens. All of our monkeys had previously been trained to exchange small metal or plastic tokens with human experimenters for food rewards. In experiment 4, monkeys could choose to exchange a token with one of two experimenters, both offering the same food reward (a small piece of marshmallow). During the first token exchange session, monkeys did not prefer either experimenter for their token exchanges [mean, 4.55 and 5.15 exchanges; $t(9) = -0.25$, $P = 0.81$] (Fig. 3). Immediately after this first token exchange session, we replicated experiment 1. During the baseline imitation phase, monkeys did not visually discriminate between the experimenters [mean, 37.25 and 40.19 s; $t(9) = -0.93$, $P = 0.37$]. During the experimental imitation manipulation, monkeys showed a visual preference for the imitator during imitated actions [$t(9) = 3.12$, $P = 0.012$] (Fig. 2). Finally, we conducted a second token exchange session, in which monkeys could choose to exchange a token with either the imitator or the non-imitator, again receiving the same food reward from both experimenters. Monkeys now exchanged significantly more frequently with the imitator [mean imitator, 6.05; mean non-imitator, 4.95 exchanges; $t(9) = 2.30$, $P = 0.047$] (Fig. 3), indicating that being imitated increased the frequency of the monkeys' interactions with the imitator.

To confirm that, like the proximity measurements, the token exchanges were not merely

facilitated by increased familiarity or perceived attentiveness of the imitator, we ran experiment 5 as a control study. At the start of experiment 5, monkeys could exchange tokens with one of two experimenters, who offered identical food rewards. As in experiment 4, monkeys initially did not prefer either experimenter [mean, 4.55 and 5.45 exchanges; $t(9) = -0.95$, $P = 0.37$] (Fig. 3). We then replicated the gaze control manipulation from experiment 3; that is, one experimenter faced and looked directly at the monkeys, whereas the other experimenter turned around and faced away from the monkeys, which led to monkeys looking significantly longer at the experimenter facing them [$t(9) = 3.51$, $P = 0.007$] (Fig. 2). A second token exchange session, which immediately followed the manipulation phase, revealed, however, that monkeys did not prefer to exchange tokens with the experimenter who had faced them during the manipulation phase [mean looking at monkey, 4.8; mean looking away from monkey, 5.2 exchanges; $t(9) = -0.49$, $P = 0.64$] (Fig. 3). Experiment 5 therefore confirms that it is the process of being imitated that led to increased interactions with the imitator.

These experimental results demonstrate that imitation significantly affects the behavior of capuchin monkeys: They look longer at imitators, spend more time in proximity to imitators, and prefer to interact with imitators in a token exchange task. As control experiments 3 and 5 show, these behavioral preferences cannot be

solely explained by familiarity or the perceived attentiveness of the imitator. Thus, imitation positively affects subsequent social interactions not only in humans but also in capuchin monkeys.

Increased affiliation in human studies is observed after the matching of subtle gestures (2, 5) or synchronized movement between individuals (18), not the conspicuous imitation shown in the present study. Moreover, it is generally accepted that capuchins do not explicitly match actions in the precise and timed manner of the human imitator in the present study (9, 15, 19). How well do these effects, which were observed under controlled laboratory conditions, transfer to capuchins' natural group environment? Precise data on this phenomenon in group settings are clearly needed, but it is known that wild capuchin groups routinely synchronize their behavior; for example, for travel, feeding, and predator defense (15). It is possible that such group synchronization may provide a sufficient degree of behavioral matching to produce positive effects on subsequent social interactions. Moreover, monkeys are unlikely to understand others' intentions to imitate them (SOM text) (8), so that explicit and implicit matching of behaviors are likely to affect them in similar ways. Matching or synchronization of behaviors may therefore carry substantial adaptive value not only as a mechanism of social learning (20) but also through its effects on subsequent social interactions.

It has been argued that the link between behavior matching and increases in affiliation might have played an important role in human evolution by helping to maintain harmonious relationships between individuals (21). We propose that the same principle also holds for other group-living primates. Matching or coordination of behaviors may lead to higher levels of tolerance and affiliation as well as decreases in aggressive behaviors, thereby increasing group cohesion. Behavior matching can therefore be regarded as a type of "social glue," helping to bind individuals together (21). The effects of behavior matching are not necessarily restricted to only two interaction partners, but may also lead to prosocial behaviors toward other individuals who were not directly involved in the social imitative exchange (3). An empathic connection resulting from behavior matching (2) may therefore extend to others in the social environment and promote altruistic behavioral tendencies in capuchins (22) and humans (3, 4).

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Mindblind Eyes: An Absence of Spontaneous Theory of Mind in Asperger Syndrome

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Adults with Asperger syndrome can understand mental states such as desires and beliefs (mentalizing) when explicitly prompted to do so, despite having impairments in social communication. We directly tested the hypothesis that such individuals nevertheless fail to mentalize spontaneously. To this end, we used an eye-tracking task that has revealed the spontaneous ability to mentalize in typically developing infants. We showed that, like infants, neurotypical adults' (n = 17 participants) eye movements anticipated an actor's behavior on the basis of her false belief. This was not the case for individuals with Asperger syndrome (n = 19). Thus, these individuals do not attribute mental states spontaneously, but they may be able to do so in explicit tasks through compensatory learning.

Impairment in reciprocal social interaction and communication is a core feature of autism spectrum disorders, regardless of age and ability. This core feature is manifest in a wide range of social impairments, including characteristic deficits in comprehension and use of pretend play, expressive gestures, deception, and irony (*1*). One influential account that can explain these varied and characteristic impairments proposes that they are a consequence of a failure in the neurologically based capacity to "mentalize," that is, the automatic ability to attribute mental states to the self and others. The first evidence for this hypothesis, which is also known as a deficit in theory of mind (ToM) or "mindblindness" (*2, 3*), comes from the finding that children with autism fail the verbally instructed Sally-Anne false-belief task (FBT), whereas 4-year-old neurotypical children pass, as do children with Down syndrome of similar verbal mental age (*4*).

In this task, which is considered a stringent test of ToM (*5*), one character (Sally) places a marble in a basket and leaves the room. In her absence, another character (Anne) moves the marble to a box. When Sally returns, children are asked where she will look for her marble. If children understand that Sally's actions will be based on what she believes to be true, rather than the actual state of affairs, they should answer that she will look in the basket, rather than the box. This correct answer requires the child to predict Sally's behavior based on her now false belief.

Despite still exhibiting atypical social features characteristic of autism, individuals of higher verbal ability, in particular those with Asperger syndrome, can pass such false-belief attribution tasks (*6–9*). This competence presents a puzzle for the mindblindness hypothesis (*10*) and has prompted the proposal that these high-ability individuals have acquired the ability to reason explicitly about false beliefs by compensatory learning, whereas difficulties in spontaneous mental-state attribution may nevertheless persist (*11*). To date, there is only indirect evidence in support of this hypothesis (*12–16*). In this study, we seek to provide direct evidence by contrasting the ability to pass the standard FBT with spontaneous looking behavior during a nonverbal form of this task.

In a groundbreaking study, Onishi and Baillargeon (*17*) used an FBT scenario to exploit infants' tendency to look longer at events that they do not expect. The authors showed that 15-month-old infants looked substantially longer when an actor searched in a location where an object was hidden that she could not know about (that is, when her behavior was incongruent with her belief). Southgate *et al.* (*18*) extended this paradigm so that, rather than measuring whether young children look longer at unexpected outcomes, they measured whether children actually anticipate the outcomes before they happen. They designed a task that made it possible to assess directly whether children had an understanding of the content of an actors' belief. Briefly, 25-month-old children were familiarized to an event in which a puppet hid a ball in one of two boxes (Fig. 1A), and then an actor reached through one of two windows to retrieve the ball from the box (Fig. 1C). Before she reached, a light and simultaneous chime signaled that the actor was about to open a window to retrieve the hidden object (Fig. 1B). In the test trial, the puppet transferred the ball from one box to another and then removed it altogether while the actor was looking away (Fig. 1D). An eye tracker was used to assess whether children expected (by making anticipatory eye movements) the actor to open the door, which would be consistent with her having a false belief about the location of the ball. Southgate *et al.* found that these typically developing children made eye movements toward the window above the box, which was consistent with the actor's belief about the location of the ball, despite the fact that it no longer contained the ball. These children, who would not be able to perform the traditional verbally instructed FBT, thus correctly anticipated the actor's behavior in line with her false belief.

It is this task (detailed above) that we used for the present study (see also movies S1 and S2). We asked whether adults with Asperger syndrome would, through their anticipatory looking, reveal a similar spontaneous capacity for false-belief attribution. At the same time, we had to establish that neurotypical adults would show the same anticipatory looking as young

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