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Review article

Social modulation of cognition: Lessons from rhesus macaques relevant to education

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ABSTRACT

Any animal, human or non-human, lives in a world where there are others like itself. Individuals' behaviors are thus inevitably influenced by others, and cognition is no exception. Long acknowledged in psychology, social modulations of cognition have been neglected in cognitive neuroscience. Yet, infusing this classic topic in psychology with brain science methodologies could yield valuable educational insights. In recent studies, we used a non-human primate model, the rhesus macaque, to identify social influences representing ancient biases rooted in evolution, and neuroimaging to shed light on underlying mechanisms. The behavioral and neural data garnered in humans and macaques are summarized, with a focus on two findings relevant to human education. First, peers' mistakes stand out as exceptional professors and seem to have devoted areas and neurons in the primates' brain. Second, peers' mere presence suffices to enhance performance in well-learned tasks, possibly by boosting activity in the brain network involved in the task at hand. These findings could be translated into concrete pedagogical interventions in the classroom.

Contents

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1. Introduction

1.1. Neuroeducation: a promising new field

Over the past decade, there has been a tremendous interest in using findings from psychology and cognitive neuroscience to inform the practice of education. This approach, sometimes referred to as neuroeducation or educational neuroscience (Ansari et al., 2012), is grounded on the premise that knowledge about the cognitive mechanisms underlying tasks that are relevant to learning and education may lead to tangible and direct benefits in the classroom. Numeracy and literacy are the two domains that have attracted the most interest, perhaps because of the considerable progress that has been made in recent years regarding the neural circuitry underlying numerical processing and reading.

First, neuroimaging studies have shown that learning symbolic arithmetic relies on the co-option of evolutionary older neural mechanisms supporting non-symbolic quantity comparison in and around the intra-parietal sulcus (IPS) (Ansari, 2016, 2008; Dehaene and Cohen, 2007; Prado et al., 2014, 2011). This has stimulated intervention studies in which practice of non-symbolic comparison tasks has been shown to lead to improvements in symbolic arithmetic skills (Hyde et al., 2014; Park and Brannon, 2014, 2013). Arguably, such findings may have very practical implications in the classroom as they emphasize the importance of training non-symbolic numerical processing skills when children learn arithmetic.

Second, echoing research on numerical cognition, it is also increasingly believed that learning to read relies on the co-option of evolutionary older neural mechanisms sensitive to basic visual properties (e.g., line configurations) in the temporo-occipital cortex (Dehaene and Cohen, 2007), as well as brain mechanisms involved in spoken language processing in the temporal lobe (Schlaggar and McCandliss, 2007). Specifically, cognitive neuroscience research suggests that recognizing written words involves a gradient of hierarchically organized responses in the temporo-occipital cortex, with different systems responding to letters, bigrams and morphemes (Vinckier et al., 2007). Such a neural organization indicates that the brain decodes written words by breaking them down into letters and graphemes rather than by processing their global contour. This clearly supports an approach to teaching reading that would be based on grapheme-phoneme correspondences rather than whole-word recognition (Dehaene, 2009). Overall, then, there may be important educational insights to be gained from cognitive neuroscience findings.

As emphasized by several researchers, however, there is a fundamental problem with translating cognitive neuroscience findings obtained in laboratory settings to the classroom (Bruer, 1997). This is in part because cognitive neuroscience findings have overwhelmingly been collected in individuals artificially isolated from their peers. Cognitive neuroscience wrongly regards cognition as a purely individual matter where concentration and motivation suffice to reach optimal performance. It neglects the fact that, in real life, humans-like all other animals- live in a social world where conspecifics are omnipresent. This is especially the case of educational settings, where children and adolescents are in constant presence of each other and should not simply be considered a collection of individual minds. Considering this social dimension will be critical in the future if one wants to translate any cognitive neuroscience findings into successful pedagogical interventions in the classroom.

1.2. Inescapable social influences

Whatever the species it belongs to, an individual's behavior is always embedded in a social context. Others influence behavior whether their presence is actual, imagined, or implied (Allport, 1968). Even individuals that do not live in a group are under social influence. Nocturnal prosimians typically described as 'solitary' primates actually maintain well-developed social organizations via distant cues such as vocalizations and scent-marking (Müller and Thalmann, 2000). Likewise, hikikomoris, those modern-day urban hermits who, in Japan and elsewhere, shut themselves up for months or years in their room do maintain distant social interactions, in particular virtual ones via the internet (Wong, 2009). Because others are omnipresent, their influences on individuals' behavior take on many forms. This has long been established in social psychology.

"Social comparison" refers to the fact that we perform better when paired with slightly better-off peers than alone, but are inhibited by strongly better-off peers (Huguet et al., 2009, 2001; Muller et al., 2004). "Social loafing" refers to the fact that we make less effort to achieve the common goal of a group than we would to achieve the same goal by ourselves (Huguet et al., 1999a; Jackson and Harkins, 1985). "Social learning" encompasses the different ways we gain knowledge from others: imitative learning is when we duplicate another's behavior, observational learning when we use information obtained via the observation of someone else to make a decision of our own (Bandura, 1965; Bandura et al., 1966, 2006). "Social facilitation" covers all the effects upon behavior of the mere presence of another individual, which are generally positive for well-learned responses and negative for unfamiliar responses (Belletier et al., 2015; Reynaud et al., 2015; Zajonc, 1965). To date, however, the impact of these social influences on the behavioral and brain correlates of tasks that are deemed relevant to education is unknown.

1.3. Relevance of the nonhuman primate model to neuroeducation

Research with non-human primates, especially macaque monkeys, has played a major part in neuroscience for 80 years now, since Jacobsen's, 1936 princeps study on frontal functions (Passingham, 2009). Non-human primates have been important for the basic understanding of brain function as epitomized by Hubel and Wiesel's Nobel Prize-winning studies on visual information processing (Capitanio and Emborg, 2008). They also have provided invaluable insights into the causes and ways to treat or rehabilitate human neural disorders, including adulthood amnesia (Meunier and Barbeau, 2013) and childhood psychopathologies (Machado and Bachevalier, 2003). Because of the physiological similarity and phylogenetic proximity of non-human primates to humans, one can address questions that cannot be addressed using other animal models such as rodents (Bachevalier and Meunier, 2005; Phillips et al., 2014). Rodents especially lack the granular prefrontal brain

areas that appeared with primate evolution and underlie the outstanding flexibility of primate behavior (Wise, 2008). Macaques, however, are no reputed mathematicians, nor are they known for their reading skills. So how can they contribute to the emerging field of neuroeducation?

It has long been thought that the human ability for formal math emerged from language (Chomsky, 2006). However, as mentioned earlier, recent evidence from cognitive neuroscience research indicates that it might instead be grounded in non-linguistic capacities inherited from evolution, such as a "number sense" that is intertwined with spatial intuitions (Dehaene and Brannon, 2010; Amalric and Dehaene, 2016; Ansari, 2016). The concept of "number sense" describes an evolutionarily and ontogenetically ancient system that allows for an approximate representation of number without the need to count or rely on numerical symbols (Dehaene, 2001). It underlies numerosity discrimination, that is, the ability to detect which among two dot arrays contains the more dots. Numerosity discrimination is present in macaque monkeys' behavioral repertoire whether they live in the laboratory or in the wild (Cantlon, 2012; Cantlon et al., 2015; Cantlon and Brannon, 2007). Number sense depends on the IPS brain region in macaques (Nieder and Miller, 2004), as it does in humans (Piazza et al., 2004). Especially relevant to education is the fact that monkeys share this non-symbolic numerosity comparison skill with human infants, for whom it is a unique predictor of later arithmetic skills (Chen and Li, 2014; Gilmore et al., 2010; Halberda et al., 2008; Starr et al., 2013). Number sense in monkeys therefore provides insight into the primitive system constituting the foundation for arithmetic learning.

Much like math, reading is a recent cultural invention that is uniquely human. Yet, it has also been argued that the neural system subserving the visual recognition of words reuses an evolutionary precursor sustaining object recognition and shared by human and non-human primates (Dehaene, 2011; Dehaene and Cohen, 2007). Specifically, neuroimaging studies systematically point to the critical role of a brain region located in the left occipito-temporal sulcus in reading (Dehaene and Cohen, 2011). This region, termed the visual word form area (VWFA), appears to be consistently involved in the recognition of written characters across individuals and cultures. The posterior to anterior organization of responses from individual letters to morphemes in this region (Vinckier et al., 2007) may have been inherited from the hierarchical organization of neural detectors tuned to increasingly complex (or fragments of) objects in macaques (Booth and Rolls, 1998; Rolls, 2000). Overall, there is increasing evidence in favor of the hypothesis positing that uniquely human functions, not present at birth and honed during development (such as arithmetic and reading), actually 'recycle' pre-existing brain circuitry with closely related functions that are present in non-human primates (Dehaene, 2004).

Here, we propose to stretch Dehaene's recycling hypothesis to social intelligence. Social intelligence is not itself a cultural invention like reading or math, but the human refinement of social skills is. Like reading and math, it is a human specificity not present at birth and honed during development. Like reading builds upon object recognition and arithmetic upon number sense, the refined social skills of adult humans rest upon evolutionarily primitive social skills present in human infants and non-human primates. At the behavioral level, this hypothesis implies that monkeys display evolutionary precursors of uniquely human social skills. This presumption is consistent with recent behavioral studies showing a continuum in the social skills of humans and monkeys, especially macaques. Monkeys do not recognize themselves in the mirror as we do (Anderson and Gallup, 2011) but they clearly make the difference between their reflection in the mirror and a stranger (de Waal et al., 2005; Rajala et al., 2010). Despite monkeys' reputation as poor imitators (Visalberghi and Fragaszy, 2002), macaques are able to copy some of others' motor acts e.g. tongue protrusion when they are infants or hand clapping when they are adults, and they also recognize when they, in turn, are being imitated (Ferrari et al., 2006; Kumashiro et al., 2008, 2003; Paukner et al., 2009; Sclafani et al., 2014). Macaques do not have a human-like theory of mind (Martin and Santos, 2016), lacking in particular insight into others' beliefs (Marticorena et al., 2011), but they possess some understanding about what others see (Canteloup et al., 2016; Flombaum and Santos, 2005), hear (Santos et al., 2006), attend to (Canteloup et al., 2015a, 2015b) or know (Marticorena et al., 2011). Our own studies, detailed below, concur with this growing empirical evidence. They highlight the proximity of rhesus macaque to humans regarding two major social influences on cognition: observational learning (Meunier et al., 2007; Monfardini et al., 2014, 2012, 2008) and social facilitation (Monfardini et al., 2015; Reynaud et al., 2015). Combining behavioral and neuroimaging data, these studies reveal social modulations of cognition representing ancient biases rooted in evolution, and shed light on underlying neural mechanisms.

2. Observational learning

2.1. Observational learning in monkeys

Observational learning was demonstrated very early on in rhesus monkeys. It was first described over the course of pioneering studies on animal learning conducted by Riopelle and collaborators at Emory University in the late 1950s and early 60s. Two monkeys were placed on each side of a test tray equipped with two food wells. In a first experiment, the wells were covered by two different objects and the monkeys had to find out which of the two objects was rewarded, and which was unrewarded (Darby and Riopelle, 1959). In a second experiment, the wells were covered by two identical objects and the monkeys had to find out which location (left or right) was rewarded, and which was unrewarded (Riopelle, 1960). In both tasks, on each problem, the monkeys witnessed their companion execute a single demonstration trial prior to performing their own first trial. Performance reached up to 75–80% correct responses, well above the 50% chance level to be expected on a first trial, and this, especially when the demonstrator had shown the incorrect response. Except for one study (Myers, 1970), both findings, that rhesus macaques can gain some knowledge from others, and perhaps especially from others' mistakes, basically went unnoticed for decades, overshadowed by an enduring theoretical debate about where to place the human-animal divide when it comes to imitation and social learning (see e.g. Laland and Galef, 2005; Whiten et al., 2009).

With the 21st century, animal cognition research took a new turn akin to the evolution of children cognition research with Dehaene's 'recycling' hypothesis. Namely, comparative cognition now privileges the idea that uniquely human complex cognitive capacities are built upon basic building blocks that humans possess in infancy and share with many non-human animals, including monkeys, their primate cousins (de Waal and Ferrari, 2010; Gariépy et al., 2014). This fresh impetus brought in its wake a cascade of new empirical demonstrations of observational learning in monkeys. In 2004, Brosnan and de Waal studied capuchin monkeys trained to trade with the experimenter tokens for foods, some attractive (e.g. a sugary cereal) and some less so (e.g. a piece of green pepper). These animals were able to learn which among two new tokens was associated with the most desirable food, vicariously, after having witnessed 10 exchanges of the new tokens between the experimenter and an expert peer (Brosnan and de Waal, 2004). The same year Subiaul et al. studied rhesus macaques trained to touch each set of four images presented on a touch screen in a specific order. These animals learn the order associated with novel sets of images

faster after they had witnessed the demonstration of an expert peer than when they had to learn new sequences entirely by trial and error (Subiaul et al., 2004). In 2007, Meunier et al. studied rhesus macaques trained, as in Darby and Riopelle (1959), to find for each pair of objects presented on a test tray which object was rewarded, and which object was unrewarded. These animals learn novel lists, each comprising 10 pairs of objects, faster after observation of the demonstration of a novice peer than when they had to learn new lists solely by trial-and-error (Meunier et al., 2007).

Importantly, the three above studies (Brosnan and de Waal, 2004; Meunier et al., 2007; Subiaul et al., 2004) all convincingly ruled out explanations other than social transmission of knowledge. The observed performance improvements were not due to social facilitation, i.e. to the performance enhancement produced by the mere presence of a conspecific. For example, in Meunier et al.'s study the animal's companion was always present so social facilitation equally occurred for the lists learned after observation and the lists learned solely by trial and error. Nor could the observed benefits be attributed to stimulus enhancement i.e. the attention-drawing interaction of a demonstrator with a particular object. For example, in Brosnan and de Waal's study, a control condition where the experimenter simply presented the novel tokens side by side with their associated food failed to improve animals' performance. Subiaul et al. subsequently completed the demonstration of the proximity of monkeys' social learning to humans' by testing two-year-old children in the same ordinal task as that used in rhesus macaques. They showed that toddlers and macaques behave in a remarkably similar way, both of them learning the position of two of the four pictures by observation (Subiaul et al., 2007).

The above studies established that monkeys are able to monitor other monkeys' choices and their outcome and to use this knowledge to guide their own decisions. Genovesio et al. later established that macaques can also cooperate with and learn from human experimenters. Macaques learn object–reward associations or the food value of tokens faster after having witnessed the demonstration of an expert human model (Bevacqua et al., 2013; Falcone et al., 2012b). They also learn to take turns with a human in a continuous visual discrimination task, integrating the human's response to guide their next decision (Falcone et al., 2012a). Monfardini et al. identified the mediator of such cross-specific human-to-monkey transmission of knowledge: similarity. Monkeys learn from humans who behave as a monkey would, i.e. who perform a task and consume earned food rewards. They fail to learn from humans who point to the correct response leaving the reward untouched, an irrational behavior from a macaque's perspective (Meunier et al., 2007; Monfardini et al., 2014). Together, these findings opened the way to monkey studies using controlled demonstrations by human demonstrators (Isbaine et al., 2015) to explore the neural properties underpinning the monitoring of others' choices (Falcone et al., 2015). They also demonstrated that similarity between the actor and demonstrator is as critical to monkeys' social learning as it is known to be to humans' social learning. Humans can learn from many agents other than their conspecifics. They can learn from a robot or a puppet, for example, provided they perceive the robot's or puppet's behavior as resembling their own (Meltzoff, 2007). Accordingly, the brain's ventral prefrontal areas take into account the individual's subjective feeling of closeness to the other when it processes others' rewards (Azzi et al., 2012; Mobbs et al., 2009).

Taken together, recent monkey behavioral studies amply confirm Riopelle et al.' early demonstration that rhesus macaques can gain some knowledge from others (Darby and Riopelle, 1959; Riopelle, 1960). But what about these authors' second suggestion, namely, that monkeys learn especially well from peers' mistakes? The same phenomenon was later described in birds (Templeton, 1998), but stirred little interest in human psychology. Rather, social psychology focused on our peculiar difficulty to learn from our own mistakes.

2.2. Personal mistakes as bad advisors

Our life is an endless stream of choices: we have to decide what to drink for breakfast, which way to get to work, what meal to eat at the restaurant, which car to buy, whom to vote for, whom to marry, etc. Intuitively, we believe that the choices we make are guided by our personal preferences and that these preferences are stable. We drink coffee at breakfast because we prefer coffee over tea. What is much less intuitive is that the reverse also happens. Unbeknownst to us, our choices shape our preferences (Ariely and Norton, 2008). This is known since Brehm's, 1956 pioneering study on free choice (Alós-Ferrer and Shi, 2015). It occurs when we have to choose between two meals, two cars or two partners that we equally value. In such case, making a choice triggers an unconscious revaluation of our preferences. It adds value to the meal, car, or partner we chose, while reducing the value of the meal, car, or partner we rejected.

The change is mediated in the brain by a post-choice modification of the neural representation of the preference with an increase of caudate nucleus activation for the selected option, and a decrease of caudate nucleus activation for the rejected option (Izuma et al., 2010; Izuma and Murayama, 2013; Sharot et al., 2009). We chose, or think so, therefore we like, even in the extreme case of choice blindness studies, where experimenters covertly swap items (e.g. pictures of faces or varieties of jams) after subjects' choice. There the subjects, led to believe they have chosen the face or the jam that they actually rejected, change their preferences to the extent that they come to prefer the previously rejected alternative (Hall et al., 2010; Johansson et al., 2005; Sauerland et al., 2016).

Choice-induced preference change is not specific to human adults, it also exists in children and monkeys, including rhesus macaques (Egan et al., 2010, 2007; West et al., 2010), a fact suggesting ancient evolutionary and ontogenetic origins. Importantly, it does not occur when humans or monkeys observe someone else's choice, it solely occurs when they make the choice themselves, or believe they did (Egan et al., 2010; Luo and Yu, 2016; Sharot et al., 2010, 2012). As the fox in La Fontaine's fable *The fox and the grapes*. Unable to reach mouthwatering grapes, the fox is forced to give up; as soon as he reaches this decision, he modifies his preferences, suddenly finding the grapes sour and unworthy of him.

A fox, almost with hunger dying,
Some grapes on a trellis spying,
To all appearance ripe, clad in
Their tempting russet skin,
Most gladly would have eat them;
But since he could not get them,
So far above his reach the vine
"They're sour," he said; "such grapes as these,
The dogs may eat them if they please!"
Did he not better than to whine?
http://www.musee-jean-de-la-fontaine.fr.

Had the grapes been sour and the starving fox able to reach them, the opposite might have happened; the fox may have suddenly found them delicious. Why did evolution select this mechanism? What makes it adaptive? Psychology has proposed the cognitive dissonance theory that posits that humans strive for internal consistency and avoid psychologically uncomfortable internal conflicts (Festinger et al., 1956; Festinger, 1957). Comparative psychology suggests a more automatic and unconscious process shared by humans and animals alike (Egan et al., 2007; West et al., 2010). Rules of thumb, or heuristics, are adaptive short-cuts that are effective in a majority of cases, though prone to error in a few others. The I-chose-therefore-I-like rule of thumb effectively deals with

the many menial choices we have to make in daily life between equally valuable items for which we have no a priori preference. If our preferences were not automatically updated after each choice to revalue the selected item and devalue the rejected item, we, and all other animals, would have to make the same choice again, and again, and again, each time we encounter the same equally valued items. Choice-induced preference change effectively alleviates humans' and animals' burden by automatically enforcing a hierarchy among our values based on our past choices.

All rules of thumb or heuristics have a flip side. The drawback of choice-induced preference change is that it sometimes interferes with individuals' ability to correct their mistakes. We go on making ruinous repairs to an old car, or keep investing in an unprofitable business, or stay stuck in an unfulfilling relationship. Blame it in part on the preference we have developed for this car, business, or partner that we have chosen. This decision bias was dubbed by Richard Dawkins, ethologist at the University of Oxford, "the Concorde fallacy", in reference to the British and French governments' decision to keep investing money in the supersonic aircraft despite its lack of viability as a commercial airliner (Dawkins and Brockmann, 1980). This is where living in society becomes an advantage. It provides the opportunity to witness others' choices and their outcomes, and learn from them without being blindsided by the preference generated by our personal choices. To this date, no other nation, but France and England, have durably invested in a supersonic airliner. Nations, like people, seem to learn especially well from others' mistakes.

2.3. Peers' mistakes as good professors

It is easier to spot the speck in someone else's eye than to notice the log in our own, goes the saying. In 2012, Monfardini et al. demonstrated that this 'mistake inequity' bias is shared by humans and monkeys alike. Six rhesus macaques and fourteen humans, trained or instructed to find out which among two objects or pictures conceals a reward (a M&M candy or a 0.2€ coin), saw the same list of 8–9 pairs of items two consecutive times. The study measured how much subjects learn from a single exposure to a pair by measuring the percentage of correct responses on the second presentation of the list. Task difficulty was successfully equated across species insofar as monkeys and humans displayed indistinguishable scores (68–70% correct) when they found the correct item on the first trial. Fig. 1 summarizes the findings for the pairs whose first trial was a mistake.

When the 2nd trial followed a personal mistake, monkeys and humans were similarly biased toward following their choice-induced preference for the unrewarded object, ignoring in the process the negative outcome of their initial choice. The only difference was the strength of the bias, humans performed *at* chance level after they made a mistake on the 1st trial, while monkeys actually performed *below* chance level. The probability to repeat one's own error, already amounting to 1/2 in humans, reached 2/3 in monkeys, a difference likely due to the greater refinement, in humans, of the brain frontal areas monitoring errors (Amiez et al., 2012; Quilodran et al., 2008).

Mistakes, unlike successes, require inferring the correct response from the incorrect one. Could this additional inference process explain monkeys' and humans' tendency to repeat their mistake? No, because monkeys and humans readily made the inference when it came to peers' mistake. There, both species displayed scores well above chance level. The only difference was again the strength of the bias. When the 2nd trial followed a peer's mistake, monkeys performed *at* a level equivalent to their top individual performance, while humans actually performed *above* their top individual performance. In humans, seeing another loose has been shown to increase the pleasure of winning, and to boost activity in the brain reward system (Steinbeis and Singer, 2013; Takahashi et al., 2009). This social emotion consisting in taking delight in others' misfortunes is called gloating (Bault et al., 2008) and has heretofore been demonstrated only in humans. It may contribute to humans' outstanding ability to learn from other mistakes.

Cognitive and social biases are predictable deviations of decisions from rationality that operate unbeknownst to subjects and irrespective of their level of intelligence (Hsee and Hastie, 2006; Kahneman et al., 1974; Sharot et al., 2011). Biases are to cognition what optical illusions are to visual perception: the side effects of otherwise effective heuristics useful in helping us deal with the world's complexity and ambiguity. As mentioned earlier, the I-chose-therefore-I-like heuristic helps deal with the many instances where individuals must choose between equally valued and valuable items. It represents a real hassle in the daily life of humans who must choose between drinks, jams, laundry detergents, dishwashers, TV sets, internet providers, to cite but a few. The 'mistake inequity' bias is the price to pay for this help. It seems a reasonable price given that the bias mainly results in non-life-threatening mistakes. It spares the choices we know to be of great importance (Hall et al., 2010) as well as our ability to learn from actual punishment (Penney and Lupton, 1961).

Many of the human cognitive and social biases have been shown to exist also in monkeys. They include the endowment effect, framing effect, intergroup bias, and loss aversion (Brosnan et al., 2007; Lakshminarayanan and Santos, 2012; Lakshminaryanan et al., 2008; Mahajan et al., 2011; Santos and Lakshminarayanan, 2008; West et al., 2010). The 'mistake inequity' bias and the 'I-chose-therefore-I-like' heuristic described here complete these findings, providing further proof of the evolutionary roots of human decision biases and heuristics (Haselton and Nettle, 2006).

2.4. Others' mistakes selective neural bases

At the neuron and neuronal population levels, there is massive evidence that observed and executed actions share the same neural code (mirror neurons, e.g. Bonini and Ferrari, 2011), as do vicarious and experienced errors and feedbacks (error/feedback-related negativity, e.g. Shane et al., 2008; van Schie et al., 2004; Yu and Zhou, 2006). At the whole brain level, it has likewise been established that the same medial frontal cortex areas process errors committed by oneself and errors committed by others (Behrens et al., 2008; de Bruijn et al., 2009; Shane et al., 2008).

However, given the 'mistake inequity' bias described above, the brain must treat personal and social actions and errors somewhat differently. Accordingly, a few recent studies showed that, despite the undeniable overlap evoked above, the neural underpinnings of individual and others' actions are dissociable. Falcone et al. and Yoshida et al. used single-unit recordings in macaque monkeys to investigate the role of the frontal cortex in coding the actions and goals of other agents (Falcone et al., 2015; Yoshida et al., 2011). In both cases, animals were engaged in paradigms where they had to monitor the responses of either a human or another monkey to complete the task. Group of neurons selectively encoding observed actions and goals were found in both the medial (Yoshida et al., 2011) and the lateral (Falcone et al., 2015) frontal cortex, suggesting that some populations of neurons code the other-self distinction by selectively encoding information obtained from others. In the lateral prefrontal cortex, Falcone et al. (Falcone et al., 2015) found in addition a population of neurons specifically encoding the predicted choice of another individual. In the medial prefrontal cortex, Yoshida et al. (Yoshida et al., 2012) found neurons selectively monitoring others' mistakes. Activation selective for others' errors have similarly been reported in humans at the whole brain level (Jääskeläinen et al., 2016).

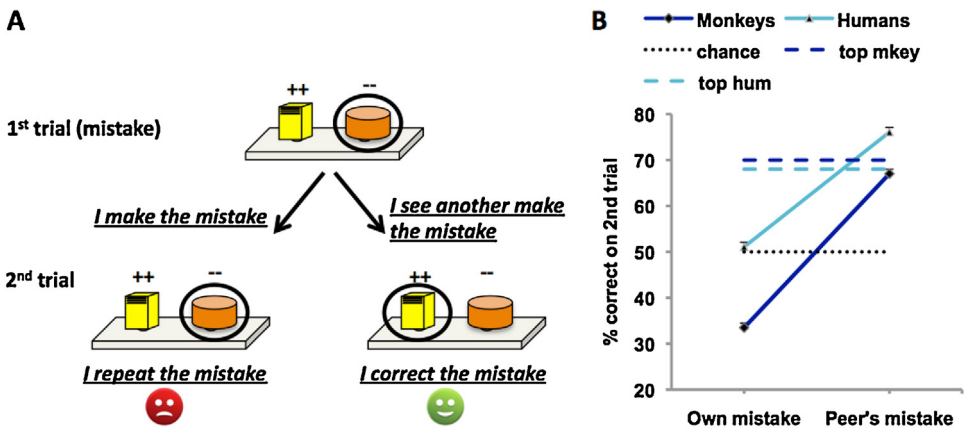

Fig. 1. Observational vs. individual learning from mistakes in humans and rhesus monkeys learning lists of pairs of objects or pictures (Monfardini et al., 2012, 2014). (A) For each pair, the subject must find out which among the two objects or pictures is rewarded (++) and which object is unrewarded (−). Theoretically, a single trial should suffice to solve the task as there are only two possible options for each pair, and executed and observed first trials should yield the same learning as they convey the very same information. As summarized here, humans and monkeys do not follow these rational predictions. The same mistake, here, selecting (black circle) the unrewarded brown cylinder, will yield different tendencies on the 2nd trial. If subjects make the mistake themselves on the 1st trial, they tend to repeat it on the 2nd trial, whereas if subjects observe the mistake of a familiar peer, they tend to correct it. (B) This 'mistake inequity' is obvious when one consider the percentage of correct responses on the 2nd trial. The same monkeys (dark blue) and humans (light blue) who perform at or below the 50% chance level (black dotted line) after their own mistake, perform well above chance after observing another's mistake. There, monkeys perform at a level equivalent to their top performance level when alone –seen as after a personal success on trial 1- (dashed dark blue line), and humans at a level above their top individual performance (dashed light blue line). Within-species paired *t*-tests for *Own* vs. *Peer's mistake*: both t's > 5.7, both p's < 0.001. Note that monkeys' *Own mistake* score is significantly below chance (one sample *t*-test, $t_5 = 4.5$, $p = 0.007$), while humans' *Peer's mistake* score is significantly above their top performance when alone recorded after a personal success (one sample *t*-test, $t_{13} = 2.9$, $p = 0.01$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The above studies show that the brain possesses neural properties and circuits devoted to monitoring others' actions and others' mistakes. But, how does the brain actually learn from others choices and their outcomes? Monfardini et al. (Monfardini et al., 2013) addressed this question using fMRI to compare the brain networks sustaining individual vs. social learning. Subjects were scanned while learning arbitrary associations either by trial-and-error or by observation of an actor. Overall, a brain network of learning-related areas was recruited during both individual and social learning conditions. This shared network also overlapped with the mirror neuron system as identified by a localizer action execution-observation task. More important here, the results (Fig. 2) also revealed brain areas that were specifically recruited during learning from others' mistakes. These areas were located in the posterior medial frontal cortex (pMFC), the left anterior insula and the bilateral posterior superior temporal sulcus (pSTS). Taken together, the knowledge accumulated by neuroscience studies in monkeys and humans suggests that the 'mistake inequity' bias, which favors learning from others' mistakes, may mirror asymmetric neural signatures where others' mistakes marshal two types of brain resources: those shared by self and others' choices and outcomes, plus those specifically dedicated to others' choices and outcomes, compared to only one type of brain resources for our own mistakes.

3. Social facilitation

3.1. The pervasive influence of others' mere presence

Among all the forms taken by social influences, the most fundamental ones are represented by the effects upon behavior of the mere presence of another individual. An observer hovering nearby indeed suffices to alter an individual's behavior, even if the observer is not interacting in any way with the observee. This phenomenon, considered as the oldest topic in social psychology, was called 'social facilitation' by Allport in 1924 (Stroebe, 2012). The name stuck although it rapidly became clear that 'social inhibition' exists as well. Others' mere presence actually facilitates the emission of well-learned responses, but impairs the acquisition of new responses (Bond and Titus, 1983 Zajonc, 1965). In a nutshell, if we are good at something, we will generally perform better in the presence of spectators. But if the task seems relatively complex to us, we will be more likely to choke in the public eye (Belletier et al., 2015; Huguet et al., 1999b).

Social facilitation occurs in presence of co-performers (coaction effect) but the presence of passive spectators (audience effect) suffices to produce the same change (Aiello and Douthitt, 2001). The effect is exacerbated when the present other represents a social threat, e.g. humans are especially inhibited by congeners expressing negative judgments (Dickerson et al., 2008) and subordinate macaques are especially inhibited by the presence of dominant conspecifics (Drea and Wallen, 1999). Social facilitation occurs, however, even with non-evaluative, non-threatening, non-interacting others (Monfardini et al., 2015). Social facilitation impacts all behaviors, whether basic such as food consumption and motor acts, or sophisticated such as cognition. We walk faster (Grindrod et al., 2006), and retrieve more well-known (verbo-verbal) associations (Fonseca and Garcia-Marques, 2013) in groups than alone. Novice golfers practice putting (Shelley-Tremblay et al., 2006) and undergraduate students learn novel (visuo-motor) associations (Belletier et al., 2015) more poorly when observed than when alone. Social facilitation is also a life-long phenomenon. Two-year-old children eat more in the presence of peers, the same remains true in hospitalized elderlies (Herman, 2015).

3.2. Social facilitation in monkeys

Social facilitation is pervasive across behaviors and ages. It is also ubiquitous across animal species. Mammals, birds, fish, and insects, all show evidence of social facilitation (Guerin, 1993). Early social psychology emphasized this 'zoobiquity' (Natterson-Horowitz and Bowers, 2012) and proposed unifying theories accounting for both human and animal data. A paradigmatic example is Zajonc's 1965 proposal that spectators facilitate the emission of well-learned responses while impairing the acquisition of novel ones. Zajonc built his demonstration upon findings from humans, chickens, rats, ants, greenfinches, parakeets, and cockroaches (Zajonc, 1965),

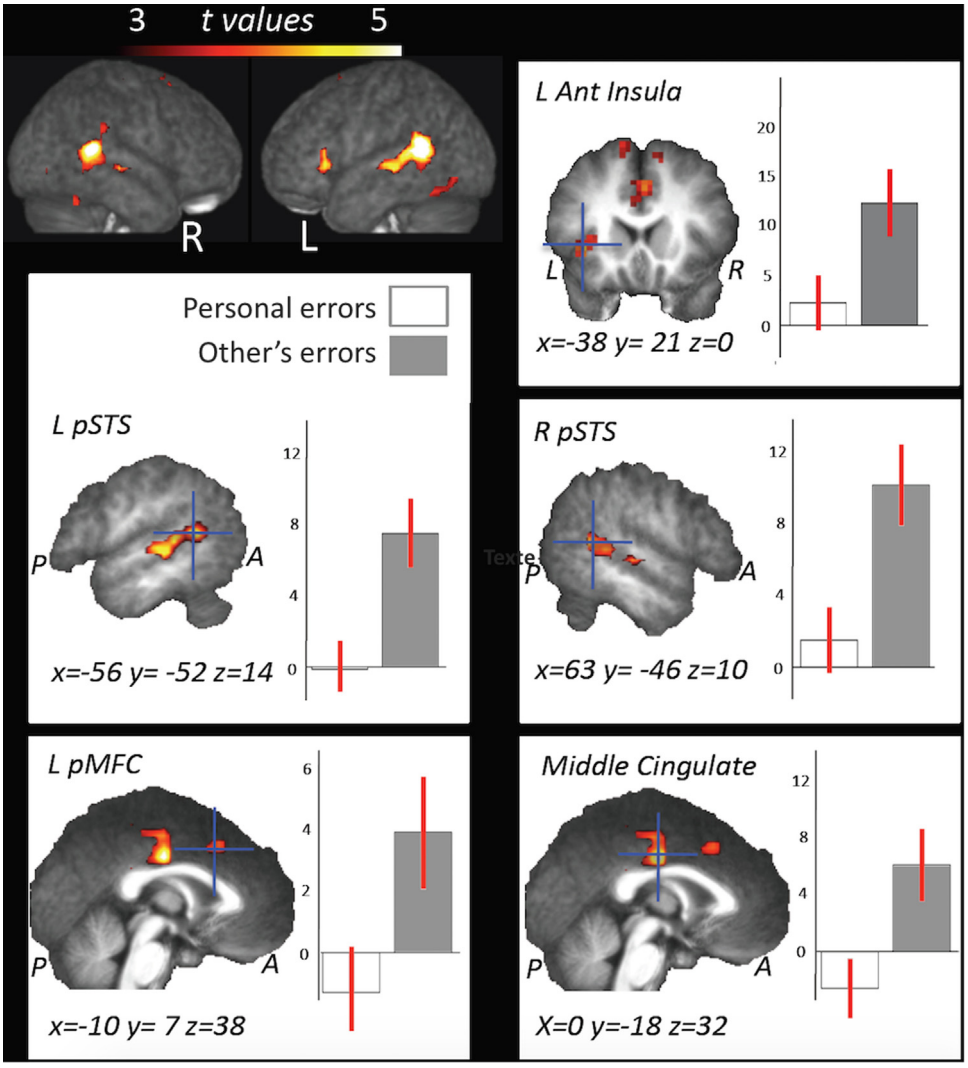

Fig. 2. Direct comparison between observed vs. personal errors during learning (Monfardini et al., 2013). Brain areas showing greater BOLD activation for processing of incorrect outcomes in learning by observation, with respect on processing of incorrect outcomes in trial-and-error learning (*Top row;* punc < 0.001, k = 15; all clusters also survive *q*FDR < 0.05). The plots of the mean value of the parameter estimates (arbitrary units) for the maxima of the activated clusters (left anterior insula, left and right pSTS, left pMFC, and middle cingulate cortex) clearly illustrate that neural circuits for personal and others' errors are dissociable in humans. Abbreviations: pSTS = posterior superior temporal sulcus, pMFC = posterior medial frontal cortex, L = left and R = right hemispheres.

believing that 'a social psychology confined to man is as parochial as a chemistry confined to gold' (Rajecki et al., 2010). By contrast, social psychology of the late 20th century tended to put forward theories relevant only to humans and to disregard evidence from social facilitation studies in animals. The evalution apprehension theory, for example, which (wrongly) supposes that social facilitation occurs only when subjects apprehend being evaluated and fear loss of face or embarrassment (see e.g. Feinberg and Aiello, 2006; Strauss, 2002 for reviews) is of little help to interpret animal behavior. In this human-centered context, social facilitation studies in animals were dismissed based, for example, on the argument that it is difficult to arrange a true 'mere presence' condition in animals (Guerin, 1993). In the mist of the recent shift of focus in comparative psychology (de Waal and Ferrari, 2010; Gariépy et al., 2014), we initiated a research program aiming at demonstrating that monkeys can help understand social facilitation and translate this knowledge into concrete applications useful to education.

Social facilitation studies in rhesus macaques are few and far between. Four have been conducted over the last 80 years. Two of them (Ferrari et al., 2005; Harlow and Yudin, 1933) show that rhesus macaques eat more in presence of co-eaters than alone, as do humans (Herman, 2015), or capuchin monkeys (Dindo and De Waal, 2007; Visalberghi and Addessi, 2000). The third one (Stamm, 1961) provided an early proof of concept that, as in humans, the presence of a co-performer in macaques affects cognition (where food serves as a reward for a task) in addition to eating (where food is simply available for consumption), a finding later replicated in capuchins (Dindo et al., 2009).

The fourth one was conducted by Reynaud et al. (2015). Seven rhesus macaques, trained to perform a simple cognitive task consisting in touching images to get food rewards, were tested alone vs. with a familiar companion serving as either an active co-performer (coaction effect) or a passive spectator (audience effect) (Fig. 3). The seven animals varied in age, gender, and social rank, and comprised one triad of lifetime companions, one dyad of adulthood companions, and one dyad of simple neighbors. The presence of a familiar companion improved performance in all animals. Response rate more than doubled relative to when the animals were tested alone. First, this was true in the coaction condition, replicating the earlier findings listed above. Second, the very same performance enhancement was observed in an audience condition. This provided an example of 'mere presence' effect in animals convincingly address-

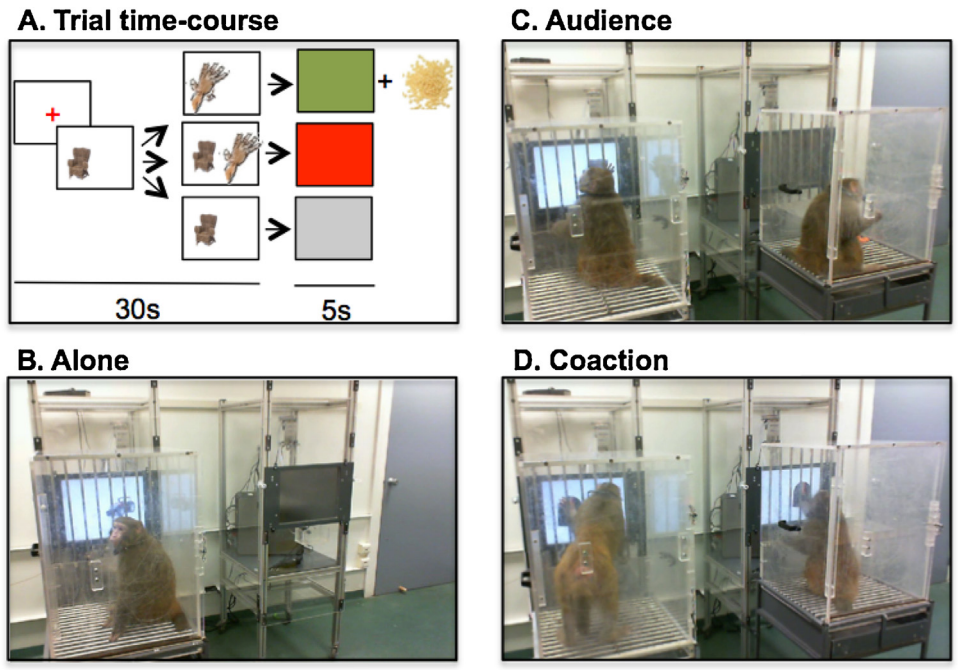

Fig. 3. (A) Trial time-course of the task used in the social facilitation studies (Monfardini et al., 2015; Reynaud et al., 2015). An image appeared on the screen. If the animal touched it within 30s, a 5 s positive feedback appeared (green screen) and a reward (dry pasta beads) was delivered. Otherwise, a 5 s negative feedback appeared (a red screen for an incorrect touch, a gray screen for a no response) and no reward was delivered. (B-D) Testing conditions. The animals were tested alone (B), in the presence of an idle companion (C) or in the presence of an active companion doing the same task (D). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

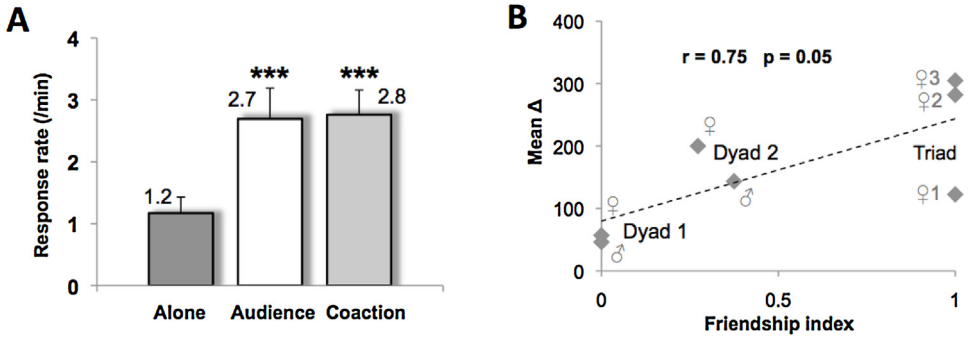

Fig. 4. Social facilitation in the 7 rhesus macaques (one triad and two dyads) included in Reynaud et al., 2015's study. The animals were trained to perform a simple cognitive task consisting in touching images to get food rewards. A. Audience and coaction. Monkeys were tested *Alone* (dark grey bar), vs. with a familiar companion serving as either an active co-performer (*Coaction*, light grey bar) or a passive spectator (*Audience*, white bar). Response rate more than doubled in the two social conditions relative to Alone, *** pairwise comparisons, p's < 0.002. B. Inter-group variability. The benefit brought by social testing (y axis; mean Δ i.e.% change between social–Audience and Coaction taken together- and solitary testing) positively correlated with the groups' degree of friendship (x axis) as measured by the ratio: years of shared housing/years of age.

ing concerns about the feasibility of mere presence experiments in animals (Guerin, 1993). Indeed, the present other was neither an ally, nor a competitor, and was of no help to solve the task at hand, so social learning (whether cueing, contagion, or imitation) could not explain performance enhancement. Social facilitation occurred (in the triad) without any decrease or increase in the cortisol response to the mild stress produced by testing, so neither a stress-buffering effect of presence (Hostinar et al., 2014) nor a stress-enhancing effect of isolation (Hawkley et al., 2012) could explain the presence effect. All seven animals were facilitated in both audience and coaction conditions, irrespective of their age, gender, social rank, and degree of friendship. Across groups (two dyads and one triad), the magnitude of the benefit seemed to increase with the animals' degree of friendship (Weinstein and Capitanio, 2012) as simple neighbors showed the smallest benefit, lifetime companions the greatest benefit, while adulthood companions fell in between. Across individuals, only two animals displayed difference across audience and coaction conditions, a subdued female was more facilitated in the unchallenging audience condition whereas an assertive male was more facilitated in the more competitive coaction condition (Fig. 4).

The social facilitation observed in macaques by Reynaud et al. (2015) fits what we know about human social facilitation in several respects. The facilitation is in line with the enhanced response rate described in simple cognitive tasks in humans (Bond and Titus, 1983). The identical effects of audience and coaction are consistent with human studies reporting equipotentiality of the two effects in the cognitive domain (e.g. Fonseca and Garcia-Marques, 2013). The moderating effect of friendship is reminiscent of similar variations reported in the human literature: e.g. co-eating strangers eat less than co-eating friends (de Castro, 1994). The moderating effect of personality traits –suggested by two of the monkeys- is in line with recent human studies emphasizing the importance of personality traits in the individual variability of social facilitation

(Uziel, 2015, 2010). Taken together, these similarities validate the idea that rhesus macaques constitute a valuable animal model of human social facilitation and that brain and behavior studies in this classical neuroscience model (Capitanio and Emborg, 2008) could help take a fresh look at one of the oldest topics in social psychology (Stroebe, 2012).

3.3. Social facilitation neural bases

Cognitive neuroscience in both humans and monkeys could be especially helpful to solve the long-standing riddle of the mechanism mediating social facilitation. This is a challenging question because it means identifying a single mechanism for both social inhibition and social facilitation. Social psychology has proposed several. As evoked earlier, some apply only to humans; they will not be discussed here (see e.g. Bond and Titus, 1983; Strauss, 2002; Uziel, 2007 for reviews). Among those holding for both humans and animals, two groups of theories stand out.

One group (anchored in behaviorism) posits that others' presence increases subjects' "drive" level (a psychological arousal with physiological markers such as cortisol; Zajonc, 1965) or simply motivates individuals to perform well (Harkins, 2006). In these motivational theories, the presence of spectators is viewed as an energizer of the most probable response, improving performance in well-learned tasks where, by definition, correct responses are dominant and deteriorating it in nonmastered tasks where errors are the most likely responses. The second group of theories (anchored in cognitivism) focus on attention rather than motivation, postulating that others' presence leads to a restriction in attention focus that is helpful (by screening out irrelevant stimuli) when the task is well-learned, but detrimental (by neglecting certain crucial stimuli) when the task is poorly learned (Baron and Kenny, 1986; Huguet et al., 1999b; Sanders and Baron, 1975). Those attentional theories rest on the counterintuitive finding that distraction, which is known to hurt performance (Pothier et al., 2014), can also improve it. Occasional distraction has been demonstrated to actually help subjects perform better during routine tasks (Cummings et al., 2013; Wierda et al., 2010). Lavie recently proposed (Lavie, 2010) that this is because tasks with low perceptual load does not use up all attention resources, thus leaving spare capacity vulnerable to interference. As a result, attention focusing actually improves under high perceptual load e.g. when distraction is added. By contrast, attention focusing deteriorates under high load on cognitive control processes e.g. tasks with high working memory demands. In this view, the presence of a social other would facilitate performance in tasks with a low perceptual load and would deteriorate performance in tasks with a high load on cognitive control.

Today, however, social facilitation research has come to an impasse because behavior alone cannot tease apart the motivation and attention (and other) hypotheses. This motivated Monfardini et al. (2015) to conduct the first neuroimaging study of social facilitation, i.e. of the performance enhancement brought by the mere presence of a peer. Three monkeys trained to touch images to get food rewards were tested alone vs. with a familiar companion. Brain activity in the two conditions was compared using [18F] fluorodeoxyglucose positron emission tomography (FDG-PET), an imaging technique compatible with ecological social testing with actual rather than virtual conspecifics. The question addressed was whether the performance enhancement brought by the mere presence of a peer, is accompanied by enhanced brain activity in the amygdalo-striato-orbital brain network regulating motivation and reward or in the fronto-parietal brain network underlying attention.

The imaging results failed to provide evidence supporting the idea that greater motivation (i.e., valuation of the reward) mediates social facilitation. No change was detected in the major nodes of the brain reward circuit: the amygdala, orbital cortex, and ventral striatum. By contrast, changes specific to the social condition occurred in a frontoparietal network linking the lateral prefrontal cortex, frontal eye field, ventral premotor cortex and intraparietal sulcus (Fig. 5). This frontoparietal attention network was already engaged in the task when animals were alone; the presence of a companion simply enhanced this task-driven activation, especially in the prefrontal component of the network. These findings therefore proved the neural validity of the attentional theory of social facilitation. They do not disprove, however, the neural validity of the motivational theory as the two are not mutually exclusive.

The findings leave two possibilities: either social facilitation systematically relies on the attention network whatever the task at hand (but then what about species devoid of fronto-parietal attention system?) or, alternatively, simply modulates activity in whatever brain substrate supports the task at hand (in the species under consideration whether mammal, bird, fish, or insect). There is no neuroimaging studies of social facilitation/inhibition in human adults to tease apart these two possibilities. However, neuroimaging studies in human adolescents, which are known to be especially sensitive to peers' influence (Steinberg, 2007), support the second possibility inasmuch as they depict neural changes induced by a peer's presence whose location in the brain vary across tasks. Dumontheil et al. (Dumontheil et al., 2016) showed that teenagers' impairment in high-level reasoning in the presence of an unknown peer is associated with increased activity in the cognitive network-comprising inferior frontal, parietal, occipito-temporal and premotor areas-underlying relational reasoning. Chein et al. (Chein et al., 2011) demonstrated that teenagers' increased risk-taking in the presence of a familiar peer is associated, by contrast, with increased activity in the ventral striatum and orbitofrontal cortex, two major nodes of the reward system that modulates risk taking. This pleads for a distributed neural coding of social context, where peer presence is capable of modifying task-related activity in several or perhaps all neural networks and systems. This speculation has two advantages. It reconciles the attention and motivation (and other) theories of social facilitation and it can apply to both human and non-human primates, as well as to other animal species.

4. Potential applications in the classroom

Education sciences constitute a dynamic field with a long history for providing educational methods to educators and policymakers. Cognitive sciences, including comparative psychology, which compares cognition and sociality across species, and cognitive neuroscience, which focuses on how the brain implements these functions, hold the promise of making two sort of contributions to the practice of education (Ansari et al., 2012; Hook and Farah, 2013). First, cognitive sciences may spark novel solutions to long-standing challenges in education. For example, by revealing the link between primitive number sense and mathematics (e.g. Starr et al., 2013), numeracy research has stimulated intervention studies in which practice of non-symbolic comparison tasks is used to improve symbolic arithmetic skills (Hyde et al., 2014; Park and Brannon, 2014, 2013). Second, and as importantly, cognitive sciences may help educators choose among (and/or refine) already available educational methods. For instance, by revealing that the brain decodes written words by breaking them down into letters and graphemes rather than by processing their global contour, literacy research clearly supports methods to teaching reading based on grapheme-phoneme correspondences, and invalidates methods based on whole-word recognition (Dehaene, 2009).

What contributions do we imagine for our results on observational learning and social facilitation? First, it is important to underline that biases, such as the mistake inequity bias, heuristics

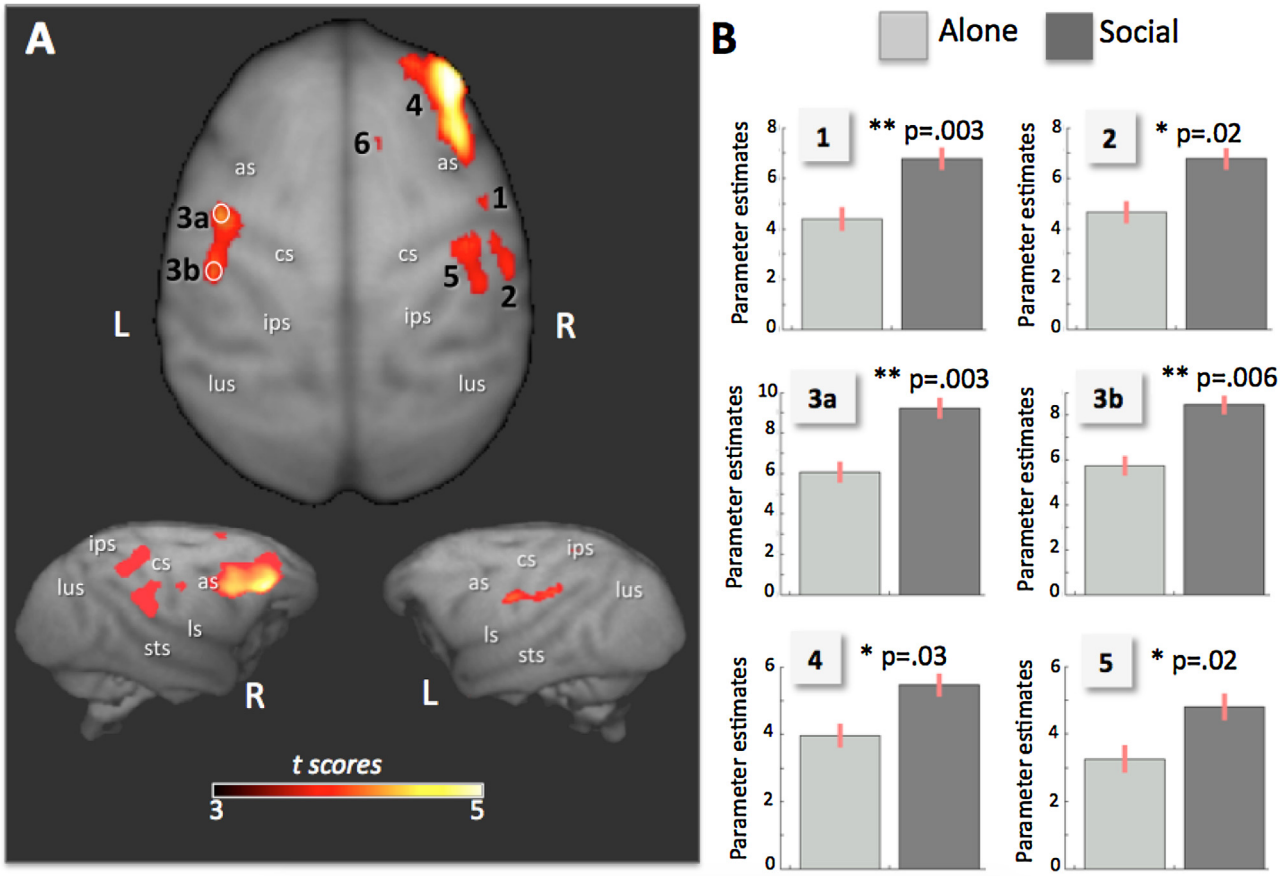

Fig. 5. Whole-brain analysis of FDG-PET data (Monfardini et al., 2015). (A) Dorsal and lateral views of the monkey brain showing the 6 task-related clusters ($t = 3.47$, $p_{unc} < 0.001$; $k = 15$). (B) Functional ROIs-based analysis of FDG-PET data reveals that all clusters but one (#6) are significantly more activated in the social than in the alone condition. In the rostral inferior parietal lobule (Area 7b or PF; #2 and 3b), the primary somatosensory area (SI; #2 and 3a), and the ventral part of the primary motor cortex (Area 4 or F1; #1 and 3a), activation is greater for the Social condition bilaterally. In the IPS and the superior parietal lobule (SPL, area 5 or PE; #5), the FEF, the lateral prefrontal cortex (lPFC, areas 45 and 46), and the ventral premotor cortex (PMv, Area F5; #4), activation is greater for the social condition only in the right hemisphere. Abbreviations: cs = central sulcus, ps = principalis sulcus, as = arcuate sulcus, ips = intraparietal sulcus, sts = superior temporal sulcus, lus = lunate sulcus, L = left and R = right hemispheres.

such as the I-chose-therefore-I-like heuristic, and social influences such as social facilitation, are all phenomenon that are deeply rooted in evolution, as demonstrated by their presence in monkeys. It means that they are exceedingly difficult, and perhaps even impossible, to overcome. They operate unconsciously irrespective of the subjects' intelligence. Awareness of, and knowledge about them are no protection. Even experts in the domain such as the present authors do display them. So the first lesson is that it is useless to try and suppress them. Awareness and knowledge are useful, however, because they empower us to seek or avoid them at will. Namely, one should seek others' presence when feeling at ease with the task at hand, and actively avoid it when feeling less competent. One should take one's preferences with a grain of salt when they do not concern issues of primary importance in life and, when in doubt, take every opportunity to gain different insight by observing others' choices and their outcomes. These basic principles can be translated inside the classroom into steps taken to minimize peers' presence when new learnings are acquired, and promote correction procedures focusing on the correction of others' mistakes.

Second, our findings may provide scientific evidence in support of some aspects of existing educational practices, in France and elsewhere in the World. One example is the French pedagogical initiative called *Twictée*, which was recently invented by two French educators, Régis Forgione et Fabien Hobart. They revisited the old-fashioned dictation using the social network Twitter, hence the name Twictée, the contraction of Twitter and *dictée* the French word for dictation (https://twitter.com/TwicteeOfficiel). The principle is to swap 140-character-dictations across classes. Two French-speaking classes somewhere around the World write a dictation, then each group of 3–4 pupils work together to produce the best dictation possible. The 7–8 dictations thus produced by each class are swapped over, so that one class corrects the dictations of the other class, again via Twitter. Teachers who have tried Twictée report spelling progress in their pupils (Rachedi, 2015). Of course, why this method works needs to be properly tested. The reasons are surely multiple (using Twitter is fun, making an active contribution is stimulating), but we predict that one of them is the fact that Twictée requires children to correct others' errors rather than their own.

Other examples of existing educational practices that are supported by our findings are pedagogical techniques minimizing the undesirable effect of peers' presence, such as flipped classrooms and environments that facilitate individualized learning. Flipped classrooms reverse the traditional organization of homework and school activities (Rotellar and Cain, 2016). Pupils familiarize themselves with the content of the lesson at home, via e.g. videos prepared by the teacher. The day after, the content of the lesson is used in the classroom under the guidance of the teacher. This reversed organization fits perfectly with what we know about the effects of social facilitation. Peers' presence in the classroom mostly interferes with the acquisition of new knowledge. De novo acquisition may thus be more appropriate as homework. Expressing newly acquired knowledge may on the opposite benefit from peers' presence, and may therefore be more appropriate as a classroom

activity. Another environment that might minimize the undesirable effect of peers' presence is an organization of the classroom that leaves some space for individual work in addition to the spaces devoted to group activities. This can be done by avoiding the customary rows of school desks, which maximize both social inhibition and social comparison, to favor classroom arrangements that include open areas where a child can settle in alone, and enjoy relative isolation from peers. This type of organization is already used in some educational approaches, such as Montessori education.

Ethics

Monkey experiments reported here were carried out in accordance with the European Directive on the protection of animals used for scientific purpose in force at the time they were carried out (Directive 86/609/EEC before 2013, Directive 2010/63/EU thereafter). Human experiments were carried out in accordance with European Directive 2001/20/EC on clinical trials.

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Conflict of interest statement

The authors declare that the manuscript was written in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author agreement/declaration

All authors have seen and approved the final version of the manuscript being submitted. The authors declare that the article is an original work, has not received prior publication and is not under consideration for publication elsewhere.

Permission note

Permission has been received to use figures in the current manuscript.

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