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ORIGINAL ARTICLE

Others' Sheer Presence Boosts Brain Activity in the Attention (But Not the Motivation) Network

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Abstract

The sheer presence of another member of the same species affects performance, sometimes impeding it, sometimes enhancing it. For well-learned tasks, the effect is generally positive. This fundamental form of social influence, known as social facilitation, concerns human as well as nonhuman animals and affects many behaviors from food consumption to cognition. In psychology, this phenomenon has been known for over a century. Yet, its underlying mechanism (motivation or attention) remains debated, its relationship to stress unclear, and its neural substrates unknown. To address these issues, we investigated the behavioral, neuronal, and endocrinological markers of social facilitation in monkeys trained to touch images to obtain rewards. When another animal was present, performance was enhanced, but testing-induced stress (i.e., plasma cortisol elevation) was unchanged, as was metabolic activity in the brain motivation network. Rather, task-related activity in the (right) attention frontoparietal network encompassing the lateral prefrontal cortex, ventral premotor cortex, frontal eye field, and intraparietal sulcus was increased when another individual was present compared with when animals were tested alone. These results establish the very first link between the behavioral enhancement produced by the mere presence of a peer and an increase of metabolic activity in those brain structures underpinning attention.

Key words: audience, FDG-PET, macaque monkeys, social facilitation, social presence

Introduction

"The influences of individuals on each others' behaviour take on very complex forms, such as group decision making, competition, or conformity to a group norm. But the fundamental forms of interindividual influence are represented by the consequences upon behaviour which derive from the sheer presence of other individuals." (Zajonc 1965).

The discovery that others' sheer presence affects individual performance dates back to the 1880s (Stroebe 2012) and has

been a topic of interest to social psychologists since then (Aiello and Douthitt 2001). The change produced by others occurs even though the "present other" is not giving cues, delivering reinforcement, exerting evaluative or competitive pressure, or lending help (Platanía and Moran 2001). It is a ubiquitous form of social influence (Guerin 2009) observed in many animals (insects, birds, and mammals) in addition to humans and affecting most behaviors, whether basic (e.g., food consumption, sexual behavior) or sophisticated (e.g., attention, memorization,

categorization). This phenomenon is called “social facilitation” (Allport 1924). The name stuck although it rapidly became clear that “social inhibition” exists as well. Empirically, the rule of thumb that remains widely accepted to this day is that the emission of well-learned responses is facilitated by the presence of spectators, while the acquisition of new responses is impaired (Zajonc 1965; Bond and Titus 1983). What remains uncertain though despite a century of effort is the mechanism by which others’ presence exerts its effect on behavior. Some theories posit 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. Other theories 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 (Sanders and Baron 1975; Baron 1986; Huguet et al. 1999, 2000, 2004; Muller et al. 2004; Sharma et al. 2010). Those attentional theories rest on the counterintuitive finding that distraction, which is known to hurt performance (Pothier et al. 2014), sometimes improves it. For example, during routine tasks, occasional distraction actually helps subjects perform better (Wierda et al. 2010; Cummings et al. 2013). Today, however, social facilitation research has come to an impasse. Behavior alone cannot tease apart the motivation and attention (and other) hypotheses. Zajonc’s (1965) idea of increased production of cortisol as an evidence of increase drive in others’ presence remains mostly untested, and psychophysiological studies focused on other markers such as heart rate or skin conductance have yielded only mixed evidence (Bond and Titus 1983; Guerin 2009). As for the neural bases of social facilitation, they have yet to be explored.

Neuroscience has provided substantial insight into the way the brain takes into account the social context. Single-cell recordings in monkeys convincingly demonstrated that the passive view of others’ actions influences cellular brain activity in several areas, including the premotor cortex (ventral part: di Pellegrino et al. 1992; dorsal part: Cisek and Kalaska 2004), the primary motor cortex (Tkach et al. 2007), and the parietal lobule (Fogassi et al. 2005). Moreover, motion-related cell activity in the monkey’s parietal and premotor cortices is modulated by social context (Fujii et al. 2007, 2008). In humans, neuroimaging studies did show different brain activity in gamers playing with another player versus with a computer or alone (Nawa et al. 2008; Fareri et al. 2012; Kätsyri et al. 2013). However, to our knowledge, no human or animal study has ever investigated the changes in brain activity accompanying social facilitation, that is, the changes associated with a behavioral improvement produced by the mere presence of a conspecific.

Not knowing the mechanism by which social facilitation exerts its effect represents a major obstacle in today’s world where social presence has become the holy grail in many domains such as e-teaching, computer-mediated communication, and marketing (Biocca et al. 2003). Identifying the neural substrates of social facilitation could fill this gap. Motivation engages a ventral brain network, the “reward network,” which includes the orbitofrontal cortex, amygdala, and ventral striatum (Haber and Knutson 2010). Visuospatial attention engages a dorsal brain network, the “frontoparietal network,” which connects

frontal areas, including the premotor and lateral prefrontal cortex, to the parietal cortex, in particular the intraparietal sulcus (IPS) and the posterior parietal lobe (Corbetta and Shulman 2002; Buschman and Miller 2007). Locating the neural changes that accompany the performance enhancement induced by another’s mere presence should therefore provide compelling evidence in favor of either the motivation or the attention theory of social facilitation.

Here, we tested this idea in the rhesus monkey, one of our closest relatives and a major animal model in neuroscience. Rhesus macaques are sensitive to social facilitation (Stamm 1961), have been at the heart of social neuroscience since mirror neurons have been discovered in their brain (di Pellegrino et al. 1992), and provide invaluable insight into robust social biases that arose through evolution and operate across species regardless of the level of language, culture, or intelligence (Monfardini et al. 2012, 2014). Three studies were conducted in 3 female rhesus monkeys trained to perform an easy task consisting in touching images on a screen to get a reward. Behavioral Study I aimed at confirming the existence of a social facilitation phenomenon in the present paradigm. Neuroimaging Study II tested whether social facilitation engages the motivation or the attention brain network. To explore the brain, we used [¹⁸F]fluorodeoxyglucose (FDG) positron emission tomography (PET), an imaging technique which—unlike functional magnetic resonance imaging for example—is compatible with ecological social testing with actual rather than virtual conspecifics. Finally, psychophysiological Study III measured testing-induced elevation of plasma cortisol to determine whether the present animals experienced: 1) equal stress in the 2 conditions, 2) greater stress under social testing, as originally predicted by Zajonc in his 1965 seminal paper (Zajonc 1965), or 3) greater stress under solitary testing, in agreement with the large body of data accumulated since then showing that isolation is stress enhancing (Cacioppo et al. 2011; Hawley et al. 2012) and social presence stress buffering (Hennessy et al. 2009; Hostinar et al. 2014) for social species.

Methods

The project was carried out in strict accordance with European Union Directive 2010/63/UE on the protection of animals used for scientific purposes after approval by the local Committee on the Ethics of Experiments in Animals (CEEA n°42 CELYNE).

Subjects

The subjects were 3 experimentally naïve 4-year-old female rhesus monkeys (*Macaca mulatta*) housed together since birth. They had free access to water and received normal daily food rations (110–130 kcal/kg/day) after testing completion. During testing, rewards were dry pasta beads rather than candies to minimize the amount of ingested glucose during PET imaging. As it takes laboratory monkeys several weeks to get used to experimental training (Lee et al. 2013), the present animals were familiarized with handling and testing procedures for 4 weeks before the present series of experiments. During this habituation period, they were also taught to cooperate with intravenous injections and blood sampling using positive reinforcement “clicker” techniques (Coleman et al. 2008).

Anatomical MRI

A structural T₁-weighted MRI scan was acquired for each monkey using a 1.5-T Siemens Sonata MRI scanner (MPRAGE sequence, TR 2160 ms, TE 2.89 ms, isotropic 0.6 mm voxel size). Skull

stripping of the brain was performed using AFNI (Cox 1996). An ad hoc template with the 3 MRI was created with the procedure described in Ballanger et al. (2013). The coordinates 0 of the template MRI, as denoted in x, y, z (mm), referred to the mid portion of the anterior commissure (ac) as an origin and the line connecting the ac and the posterior commissure (pc) as a y-axis (Frey et al. 2011).

Task and Set-up

An image (10 × 15 cm) appeared on the screen (Fig. 1B). If the animal touched it within 30 s, a positive feedback appeared (the screen turned green for 5 s) and a reward (~5 tiny beads of dry pasta) was delivered. If the monkey either failed to respond within 30 s, or touched the screen outside of the image, a 5 s negative feedback appeared (a red screen for a no response, a grey screen for an incorrect touch) and no reward was delivered. Intertrial intervals lasted 2 s. Each trial thus lasted a minimum of 7.5 s, allowing a maximum response rate of 8 responses/min. The same 7 pictures of neutral objects (e.g., a rainbow, an armchair) were used throughout all testing phases (habituation, behavioral Study I, FDG-PET Study II, and cortisol Study III). The pictures were pseudo-randomly presented on the right or on the left side of the screen (12 cm from the center), but always appeared in the same order. Each daily session lasted

15 min during Study I and 30 min during Studies II and III as 30 min is the optimum time for FDG neuronal uptake (Miyazawaa et al. 1993). All 3 animals knew the task principle and had experienced both the Alone and Social conditions by the time Study I was initiated. The selected task is very simple for monkeys taxing only motivation for the food reward and attention to the images on the screen whenever they are on.

Two 17 in. touch screens (AccuSync LCD93 V 19"), each equipped with its own computer, reward dispenser (Med Associates Mini M&M dispenser) and reward receptacle, were placed side by side, about 50 cm apart, in a large testing room (3 × 4 m). Two animals could thus be placed in the room, each in a plexiglas transport cage (60 × 60 × 60 cm) placed approximately 30 cm from a screen. Each monkey could see and hear the other one but could not reach the other's screen or rewards (Fig. 1A). The experimenter left the testing room once the monkeys were positioned, monitoring the experiment from an adjacent room. Each testing session was video recorded.

Study I: Behavior

Animals were tested 1 day alone, 1 day with 1 housemate, and 1 day with the other housemate over a total of 30 sessions.

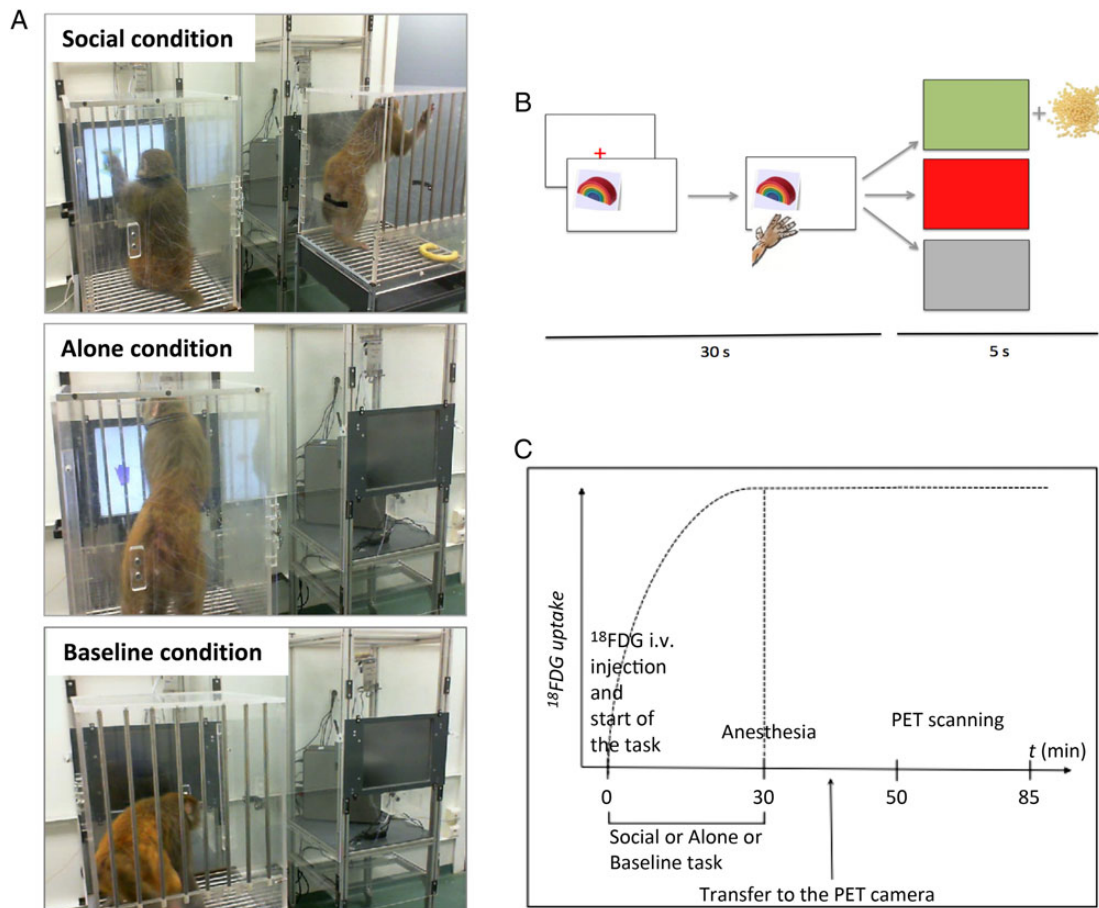


Figure 1. (A) Pictures illustrating the 3 possible testing conditions: Social, that is, the monkey is performing the task in the presence of a passive companion; Alone, that is, the monkey is performing the task while alone in the testing room; Baseline (used only in FDG-PET Study II), that is, the monkey is placed in the testing room without task or companion. (B) Task: an image was presented on the screen. If the animal touched it within 30 s, a 5 s positive feedback appeared (green screen) and a reward (dry pasta) was delivered. Otherwise, a 5 s negative feedback appeared (a red screen for a no response, a gray screen for an incorrect touch) and no reward was delivered. (C) Time course of FDG-PET sessions. PET imaging session consisted in 2 parts. A first 30-min period, starting with the saphenous injection of [^{18}F]FDG, was conducted outside the scanner. During this period, the animals either performed the task (Alone or Social conditions) or were in a Baseline condition. At the end of the 30 min of FDG uptake, the animals were anesthetized, transported to the imaging center, and positioned in the scanner to perform the PET imaging.

Response rates, that is, the number of responses per minute, were compared in the Alone versus the Social conditions using a 1-tailed paired *t*-test. The size of the social facilitation effect was evaluated using Cohen's *d* (Cohen 1988), one of the most common metric used in psychology to compare effects' magnitude across studies. Cohen's *d* expresses the amount of difference between 2 conditions in standard deviation units: $d = (MS - MA) / sw$, where *MS* is the mean score for the Social condition, *MA* is the mean score for the Alone condition, and *sw* the pooled within-condition standard deviation. Cohen's rule of thumb for interpreting *d* values is that $d = 0.2$ represents a "small" effect size, 0.5 a "medium" effect size, and 0.8 a "large" effect size.

Study II: FDG-PET Imaging

Data Collection

We used the same FDG-PET activation method as Blaizot et al. (2000). Each PET imaging session consisted in 2 parts (Fig. 1C). A first 30-min period (FDG uptake), starting with the saphenous injection of [¹⁸F]FDG (18.5 GBq/kg), was conducted outside the scanner. During this period, the animals either performed the tasks of Study I (Alone or Social conditions) or were in a Baseline condition, which consisted in staying alone in the testing room without performing any task. At the end of the 30 min of FDG uptake, the animals were anesthetized with Zoletil 100 (tiletamine-zolazepam; 10–15 mg/kg), transported to the imaging center, and positioned in a Siemens CTI Exact HR+ (Knoxville, TN) to perform the PET imaging. A stereotaxic frame maintained the head of the animal, and an infrared pulse was used to monitor the heart rate and the blood oxygen saturation. Imaging period began (FDG scan), on average, 57 min after the [¹⁸F]FDG injection (range = 50–60 min). The emission scan lasted 35 min and was followed by a 10-min postinjection (hot) Germanium transmission scan. A segmentation technique, as included in the ECAT 7.2 software (CTI, Knoxville, TN), was applied on the hot transmission data before it was used for attenuation correction in the reconstruction process. A static, attenuation and scatter corrected FDG image of 63 contiguous slices with voxel size: 0.32 × 0.32 × 2.42 mm was reconstructed (Filtered backprojection method; matrix size = 256; ramp filter; zoom = 8.0). The spatial resolution at the center of the PET scanner is 4.5 mm full-width at half maximum measured in the NEMA conditions (Brix et al. 1997). Each monkey was scanned 3 times per condition (27 FDG-PET sessions). The 27 FDG-PET sessions were distributed along the course of Study I depending on the availability of the PET scanner. The static FDG image reflects the regional glucose metabolic consumption (CRMgl), which is itself directly related to synaptic density (Rocher et al. 2003). Glucose blood level was assessed before and after the FDG uptake period.

Image Preprocessing

Static PET images were preprocessed with SPM5 (<http://www.fil.ion.ucl.ac.uk/software/spm5/>). The 9 PET scans from the same monkey were realigned to the first scan (Realign in SPM5) and averaged. The mean brain image was extracted from surrounding tissue using AFNI (Cox 1996) and coregistered to subject's MRI (Coregister in SPM5). We used 2 approaches to analyze the static PET images, coregistered to the individual MRI: a voxel-based analysis and a ROI-based analysis.

Voxel-Based Analysis

MRIs were spatially normalized (Normalize in SPM5) to the ad hoc template. Transformations were applied to the coregistered static PET images. Spatially normalized PET images were further

smoothed using a 4 mm FWHM Gaussian smoothing kernel to be ready for a voxel-based analysis. The voxel-based statistics were performed using SPM5. In a general linear model (GLM), a repeated-measures 1-factor, 3-level analysis of variance (ANOVA) across the 3 conditions (Social, Alone, and Baseline) was computed. For voxel surviving the main-effect threshold of $P < 0.001$ (uncorrected), a post hoc *t*-contrast was computed to identify the brain network engaged by the task, that is, more active for Social and Alone versus the Baseline conditions (Fig. 4A). The *t*-parametric map was thresholded, at the voxel level, at $P < 0.001$ (uncorrected) with a minimum cluster size (*k*) of 15 voxels. The anatomical location of each activated cluster was assessed using Saleem and Logothetis's atlas of the macaque brain (Saleem and Logothetis 2012). To further explore the task-related activity map, the following complementary test was performed. Mean condition effect values (beta value of the GLM) per cluster were extracted in each significant cluster, with the MarsBar toolbox (<http://marsbar.sourceforge.net/>). On these values, a 1-tailed *t*-test assessed the increase of the Social versus the Alone condition. This identified, within task-related clusters, those that were significantly more active during the Social than during the Alone conditions (Fig. 4B). We then calculated Pearson's correlations between the mean cluster value and the duration of the task-related behaviors with a significance level set at 0.05 (uncorrected).

Anatomical ROI-Based Analysis

The MAXPROB method described in Ballanger et al. (2013) was used to segment individual MRI into 42 labeled cerebral regions. From the original Ballanger atlas, the following ROIs of the motivation ventral network were selected for analysis: the orbitofrontal cortex (OFC), the amygdala, the internal and external globus pallidum, and the ventral striatum (VS). Based on Saleem and Logothetis's (2012) and Paxinos et al.'s (2000) atlases, additional regions were manually drawn on the Ballanger atlas to subdivide frontal and parietal lobes in ROIs of the dorsal attention network. It included the dorsal (PMd) and the ventral (PMv) premotor areas, the frontal eye field (FEF), and the lateral prefrontal cortex (LPF; areas 46v/45) in the frontal lobe, as well as the IPS, the inferior parietal lobe (IPL), and the superior parietal lobe (SPL) in the parietal lobe (see Supplementary Table 3). As an additional ROI, we drew on the PET mean image the masticatory muscle, to estimate the spillover effect of the muscular tissue on the contiguous ROIs (PVE, i.e., partial volume effect evaluation, Rousset et al. 1998). For that, we calculated the geometric transfer matrix (GTM; Rousset et al. 1998) using an algorithm (Frouin et al. 2002) implemented in an in-lab-made software.

For each anatomical ROI described above, we then extracted the mean FDG value using an in-lab-made software implemented in SPM. The relative variation of the FDG activity (% change FDG) compared with Baseline was computed for the Social condition ($100 \times [FDG_{uptake_{Social}} - FDG_{uptake_{Baseline}}] / FDG_{uptake_{Baseline}}$) and for the Alone condition ($100 \times [FDG_{uptake_{Alone}} - FDG_{uptake_{Baseline}}] / FDG_{uptake_{Baseline}}$) (Fig. 5). A paired *t*-test between Social and Alone conditions compared these FDG relative variations. Finally, we computed the global gray matter mean value per scan, which was used to normalize the static FDG images in the voxel-based analysis.

Performance, Activity, and Handedness During PET Sessions

Performance, that is, the number of responses per minute, recorded during the PET sessions in the Alone versus Social condition was compared using a 1-tailed paired *t*-test. Videotapes were analyzed using The Observer XT 10 to calculate the duration of 3 mutually exclusive activities: 1) rest, that is, sitting or standing

motionless, 2) task-unrelated activities, including exploration of the environment with hands, feet, or mouth, self-directed activities, and stereotypies, and 3) task-related behaviors, namely touching the screen and picking up/eating the reward. Within task-related behaviors, we distinguished right-handed versus left-handed responses to quantify how much time each hand was used over the 810 min of activation collected (27 PET sessions \times 30 min). Each videotaped session was scored by at least one observer; a subset of sessions (12) was scored by 2 observers (interobserver reliability: $r = 0.98$, $P < 0.001$). Task-related behaviors were compared using a 2×2 , condition \times hand ANOVA. All other activities were analyzed using 1-way ANOVAs (with the Huynh-Feldt adjustment for repeated measures over conditions) followed by pairwise comparisons.

Study III: Cortisol Assays

At completion of Study II, behavioral testing was resumed, alternating 1 day alone and 1 day with one or the other member of the trio. The only difference with Study II was that blood (4 mL) was drawn from the saphenous vein both before (PRE) and after (POST) behavioral testing. The aim was to determine whether one of the 2 conditions, Alone or Social, induced a greater elevation of plasma cortisol, that is, a greater stress, than the other. We followed the same procedure as Raper et al. (2013). Samples were placed in prechilled plastic EDTA-powder-containing tubes and centrifuged at 1000g for 15 min at 4°C. Plasma was removed and stored at -80°C until assayed. Samples were collected 5.5 ± 1.4 min (mean \pm SEM) after the initial disturbance, that is, the moment the experimenter entered the room where the animal was. One to 2 cortisol measures were obtained per monkey and condition. Care was taken to test each animal at exactly the same time of the day to avoid any confounding effect of the circadian fluctuations of cortisol. All assays were performed by the Lyon Richard Vitton laboratory using a chemiluminescence immunoassay technique (Roche COBAS 6000). The POST -- PRE difference in the level of plasma cortisol was calculated for each monkey and each session. These cortisol Δ s were then compared across conditions using a 2-tailed paired *t*-test.

Power Analyses

Because we had no prior behavioral or neuronal data, we could not run prospective power analyses to determine sample size. We did run, however, retrospective analyses using Dupont and Plummer PS test (Dupont and Plummer 1998). These analyses recommend a minimal sample size of 3 animals for both behavioral (mean difference in responses/min: 2.1, standard deviation: 0.6) and neural changes (e.g., mean difference in normalized regional glucose metabolic consumption in right FEF: 0.103, standard deviation: 0.033) to reject the null hypothesis with a power 0.80, and a Type I error probability $\alpha = 0.05$.

Results

Study I: Behavior

The animals completed on average 10 (range 8–13) sessions in the Alone condition and 20 (range 19–21) sessions in the Social condition. The monkeys touched the images on the screen to obtain a food treat 3 times more often under Social than under Alone testing (Fig. 2). Responses per minute rose from 1.3 ± 0.4 to 3.3 ± 0.4 (mean \pm SEM; paired *t*-test: $t_2 = 11.51$, $P = 0.004$). There was no companion effect: the “most efficient” partner yielded 3.4 responses/min and the “least efficient” partner 3.2. As

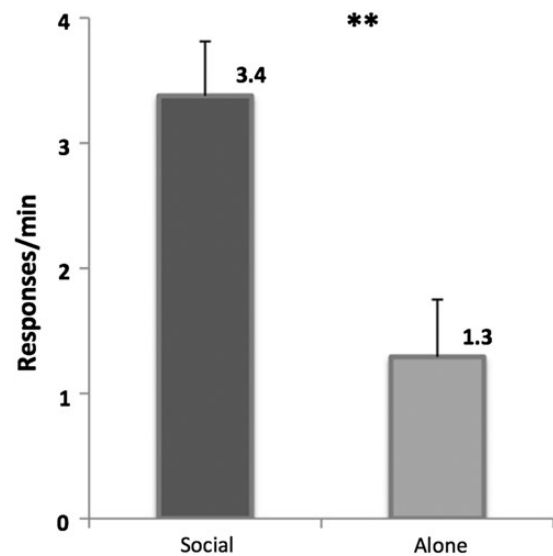


Figure 2. Performance (response rate) recorded during behavioral Study I. The monkeys touched the images on the screen to obtain a food treat 3 times more often under social than under solitary testing (** $P = 0.004$).

evaluated by Cohen’s *d*, the social facilitation observed here corresponds to an effect size of 2.6 standard deviation units, a value well above the 0.8 value generally considered as reflecting a large effect size. This marked effect made the present behavioral paradigm particularly suitable for investigating the neural and hormonal markers of social facilitation.

Study II: FDG-PET

Three sessions were conducted per animal and condition (Social, Alone, and Baseline) for a total of 27 FDG-PET sessions (3 sessions \times 3 conditions \times 3 monkeys). The glycaemia was stable and not affected by the rewards ingested during the tasks, averaging 6.0 ± 0.8 mmol/L at the time of FDG injection and 5.2 ± 1.1 mmol/L at the beginning of the scan ($t_2 = 1.92$, $P = 0.19$).

Response Rate

Response rate during the Alone versus Social FDG-PET sessions followed the same pattern as that obtained with a larger sample of sessions in Study I. It increased from 0.6 ± 0.2 to 2.6 ± 0.8 responses/min ($t_2 = 3.38$, $P = 0.04$). Effect size equaled 2.1, a value again largely superior to 0.8.

Behavior During FDG Uptake

The monkeys were equally active (as opposed to motionless) in the Alone, Social, and Baseline conditions (Fig. 3; $F_{2,24} = 0.18$, $P = 0.89$). Behavioral activity occupied two-thirds of the 30-min duration of a FDG-PET session in all cases (Alone: 19.8 ± 2.5 min, Social: 21.8 ± 2.1 min, Baseline: 19.6 ± 3.8 min). The presence of a companion simply modified the nature of activity (cf. Fig. 3). The animals dedicated more time to task-related behaviors, namely pressing the screen and retrieving rewards: 12.2 ± 2.5 min/session compared with 1.9 ± 0.8 min when alone (paired *t*-test: $t_8 = 3.6$, $P = 0.007$), and less time to task-unrelated behaviors, namely manual or oral exploration of the environment, self-directed activities, and motor stereotypies: 3.7 ± 0.7 min/session compared with 10.0 ± 2.6 min when alone ($t_8 = 2.6$, $P = 0.03$).

Voxel-Based Analysis

The voxel-wise analysis was performed on FDG uptake images using a repeated-measure 1-factor 3-level ANOVA across the Alone, Social, and Baseline conditions. On voxels exceeding the

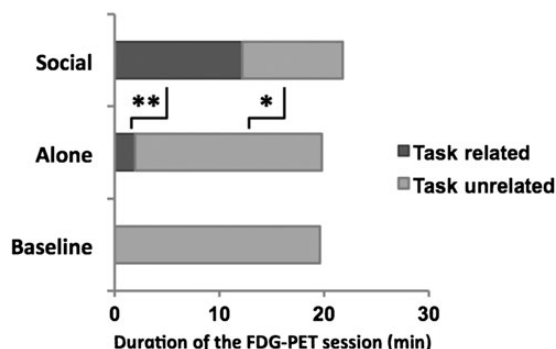


Figure 3. Behavior during the FDG-PET uptake (Study II) as quantified from the videotapes. Whatever the condition (Social, Alone, or Baseline), activity (as opposed to motionlessness) occupied two-thirds of the 30-min duration of a FDG-PET session. The Baseline condition, by definition, comprised no task-related activity. The difference between the other 2 conditions was that the animals dedicated more time to task-related behaviors, namely pressing the screen and retrieving rewards (** $P=0.007$), and less time to task-unrelated behaviors, namely manual or oral exploration of the environment with hands, feet, or mouth, self-directed activities, and motor stereotypies ($P=0.03$), when in the presence of a companion than when alone.

main effect of condition ($F_{1,52}=9.34$; $P<0.001$), a post hoc t-test contrasting Social and Alone conditions to the Baseline was performed to generate the task-related activity map showed in the Figure 4A (cf. also Table 1). We identified 6 clusters, all situated in the dorsal part of the brain. Among these clusters, all but one were significantly more activated in the Social than in the Alone condition (Fig. 4B). These clusters were located bilaterally in the rostral inferior parietal lobule (Area 7b or PF; Pandya and Seltzer 1982), the primary somatosensory area (SI), the ventral part of the primary motor cortex (Area 4 or F1; Matelli et al. 1985) and, only in the right hemisphere, in the IPS, the superior parietal lobule (Area 5 or PE; Pandya and Seltzer 1982), the FEF, the areas 45 and 46 of the lateral prefrontal cortex (IPFC), and the area F5 of the ventral premotor cortex (PMv). All these clusters of activation were positively correlated with the duration of task-related activities (cluster 1: $r=0.49$ $P=0.008$; cluster 2: $r=0.49$ $P=0.01$; cluster 3: $r=0.55$ $P=0.003$; cluster 4: $r=0.48$ $P=0.01$; cluster 5: $r=0.50$ $P=0.007$; cluster 6: $r=0.40$ $P=0.04$).

Anatomical Region of Interest-Based Analysis

We also computed an independent region of interest (ROI) analysis specifically targeting anatomical areas within the attention and the motivation networks (see Methods). The spillover effect of the muscular tissue on the contiguous cortical regions as revealed by the GTM analysis was negligible (3.7% for the closest ROI), making the partial volume effect correction not appropriate (Rousset et al. 1998).

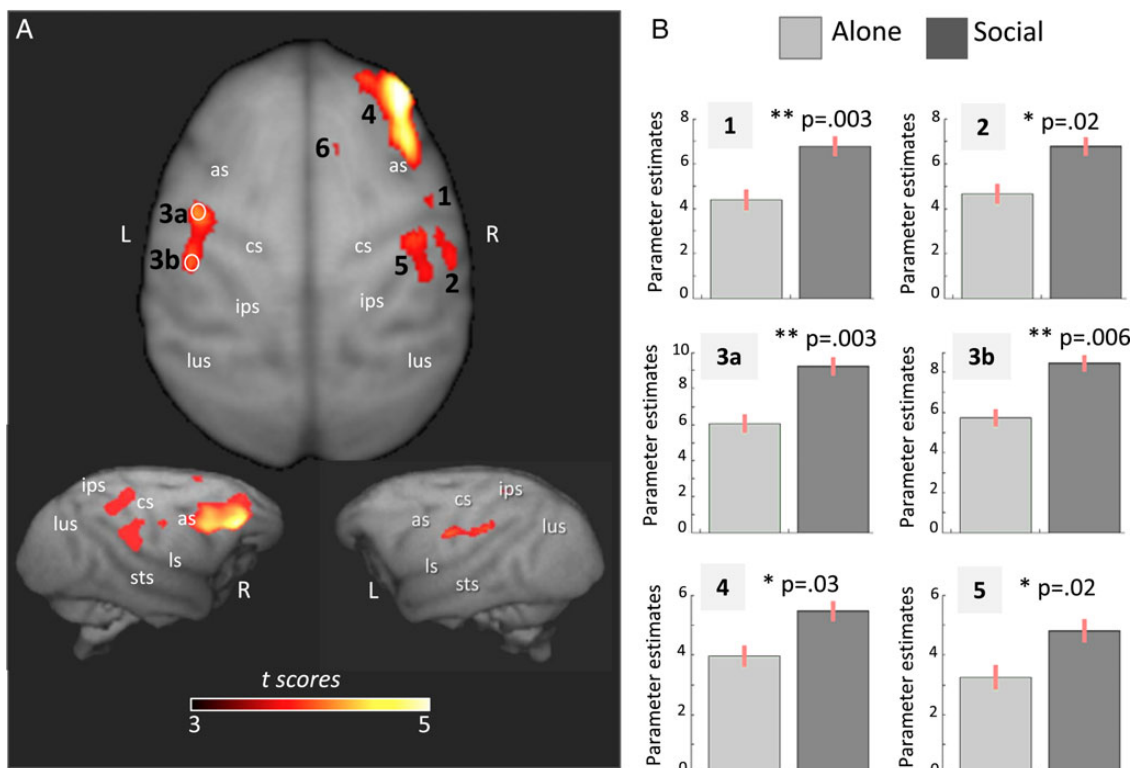


Figure 4. Study II: task-related brain activity. (A) Voxel-wise, whole-brain analysis of FDG-PET data. Dorsal and lateral views of the monkey brain showing the 6 task-related clusters ($t=3.47$, $P_{unc}<0.001$; $k=15$). Functional activations are superimposed on the ad hoc template (cf. Anatomical MRI section) using MRICron software (<http://www.mccauslandcenter.sc.edu/mricron/mricron/>). (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 (IPFC, 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.

Tables 1 Voxel-based, whole-brain analysis of FDG-PET data

Cluster name (cf. Fig. 4A)	Cluster size	Cluster P value (unc)	Peak MNI coordinates (x, y, z)	Peak P value (unc)	Peak T value	Brain area	R/L
1	27	0.257	5, 6, 19	0.001	3.67	Primary motor cortex (Area 4 or F1)	R
2	132	0.020	24, -11, 10	0.000	3.81	Primary somatosensory area (SI); inferior parietal lobule (Area 7b or PF)	R
3a	141	0.017	-19, -3, 8	0.000	4.20	Primary somatosensory area (SI); primary motor cortex (Area 4 or F1)	L
3b			-20, -13, 11	0.000	4.05	Inferior parietal lobule (Area 7b or PF)	L
4	448	0.000	16, 17, 8	0.000	5.89	Lateral prefrontal cortex (Areas 45 and 46)	R
			17, 9, 9	0.000	4.77	Frontal eye field; ventral premotor cortex (Area F5)	R
5	141	0.017	19, -10, 18	0.000	3.93	Intraparietal sulcus (LIP, AIP); superior parietal lobule (Area 5 or PE)	R
6	17	0.369	21, -2, 10	0.000	3.76	Dorsal premotor cortex (Area F2)	R

Note: Task-related clusters whose FDG uptake was superior for Social and Alone than for Baseline ($t = 3.47$, $P_{\text{unc}} < 0.001$; $k = 15$). LIP, lateral intraparietal area; AIP, anterior intraparietal area.

In line with the voxel-based analysis, the anatomical ROI-based analysis showed greater activation for the Social than for the Alone condition in 3 attention-related regions: the right LPFC, the right FEF, and the right PMv (Fig. 5B). In contrast, no differences were found across the Social and Alone conditions in the motivation-related ROIs (Fig. 5A; for more statistical details, see Supplementary Table 1).

Handedness

To determine whether the functional asymmetry in brain activation described above could result from lateralized hand use, we quantified left and right hand use during the FDG-PET uptake (Table 2). Monkey CE was left-handed (she performed 99% of the task-related actions using the left hand), monkey CA was right-handed (she performed 89% of the task-related actions using the right hand), and monkey CI was ambidextrous (she performed 51% of the task-related actions using the left hand). So, at group level, task-related hand use was evenly distributed between the 2 hands. This was confirmed by a 2×2 , condition \times hand ANOVA that yielded the expected main effect of condition ($F_{1,2} = 221.8$, $P < 0.001$) with no hand ($F_{1,2} = 0.008$, $P = 0.93$) or hand \times condition effects ($F_{1,2} = 0.02$, $P = 0.89$). In other words, there was no left hand bias in the Social condition likely to cause the right lateralization of the activation enhancement observed in the frontoparietal network relative to the Alone condition.

Summary

Study II reveals the increases in FDG uptake associated with a social presence exerting a marked facilitation effect at behavioral level. The task-related changes found to be enhanced by social presence were confined to the dorsal aspect of the brain. They concerned the right and left primary somatosensory and motor brain areas (SI and F1) and the inferior parietal lobule (PF or 7b) bilaterally, as well as a right frontoparietal attention network encompassing the LPFC, FEF, PMv, IPS, and the area 5 (or PE). No change was found within the ventral areas (the amygdala, orbital cortex, and ventral striatum) belonging to the motivation network.

Study III: Cortisol

Comparison of plasma cortisol level before and after testing showed that testing induced a mild cortisol elevation (see

Supplementary Table 2), which averaged 9.7 ± 2.2 $\mu\text{g/dL}$ (mean \pm sem) and fell short of significance (paired t -test $t_2 = -3.02$, $P = 0.09$). This testing-induced cortisol elevation was comparable across conditions, averaging 9.99 $\mu\text{g/dL}$ in the Alone condition and 9.44 $\mu\text{g/dL}$ in the Social condition (paired t -test $t_2 = 0.19$, $P = 0.87$). The behavioral and neural differences unveiled by Studies I and II can therefore be explained by neither a stress-enhancing, nor a stress-buffering effect of one or the other testing condition (Fig. 6).

Discussion

Despite the ubiquity of the phenomenon across species and tasks, the neural bases of social facilitation, the influence of others' sheer presence, are currently unknown. The present series of monkey studies addressed this issue to shed new light on the long-standing debate about the process that mediates social facilitation (motivation or attention). Study I found that monkeys trained to press an image on a screen to obtain a food treat engaged in this task 3 to 4 times more in the presence of a familiar peer than when alone. Using FDG-PET imaging, Study II showed that this social facilitation phenomenon was accompanied by enhanced task-related activation in the brain frontoparietal network of attention. Study III demonstrated that social and solitary testing induced the same mild elevation of plasma cortisol, thereby ruling out stress-related explanations of the behavioral and neuronal data of Studies I and II. Together, these data establish for the first time a link between a behavioral facilitation of performance produced by the mere presence of a conspecific and a change of metabolic activity in those brain structures underpinning attention.

Social Facilitation as a Mere Presence Effect

In his review of the social facilitation phenomenon, Guerin (2009, p. 123) pointed out that there are few studies in the animal literature truly measuring a mere presence effect. The reason for this is double. It is difficult to arrange a presence condition without cueing, contagion, imitation, or social learning of some sort. It is also difficult to arrange a solitary condition that is not a source of stress (isolation being a potent stressor to social species; Hawkey et al. 2012). The present study is an attempt to avoid both pitfalls. First, the social other was neither a coactor nor a competitor, and it was of no help to solve the task at hand. This precludes all

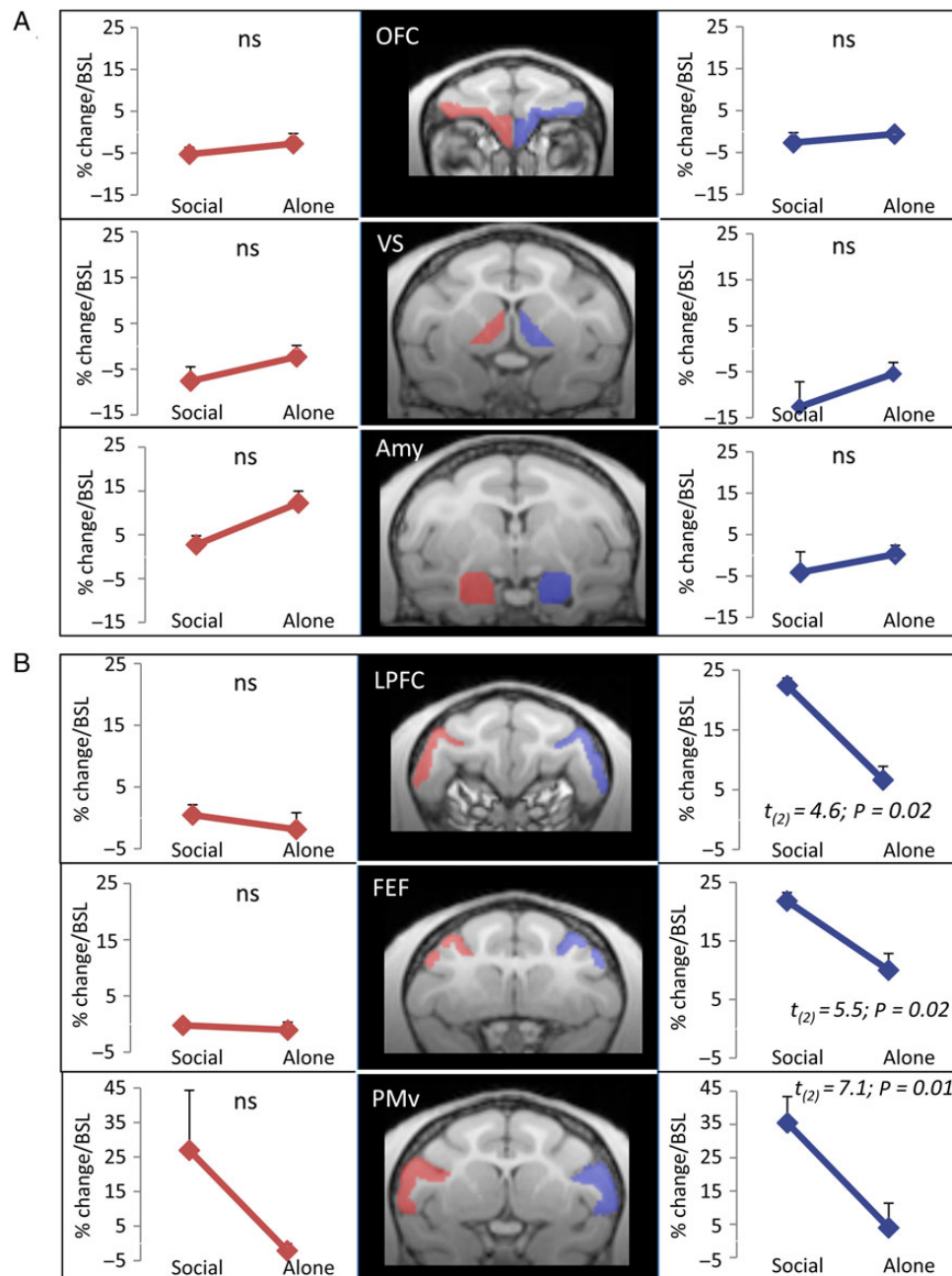


Figure 5. Study II: anatomical ROIs-based analysis of FDG-PET data. The signal percent change for Social and Alone conditions (relative to Baseline) is shown for each left (red) and right (blue) anatomical ROI within the ventral, motivation-related (A), and dorsal, attention-related (B) brain networks. For the anatomical definitions of the ROIs in A, see Ballanger et al.'s (2013) monkey MRI template: VS (Ventral Striatum), labels 5-6; Orbitofrontal cortex (OFC), labels 31-32; Amygdala (Amy), labels 23-24; External Globus pallidum (GPe), labels 7, 8; Internal Globus Pallidum (GPi), labels 9, 10. The ROIs within the attention-related dorsal network in B have been traced manually on Ballanger et al. (2013) (LPFC, lateral prefrontal cortex; FEF, frontal eye field; PMv, ventral premotor cortex; further anatomical definitions are provided in Supplementary Table 3).

forms of social transmission of information. Second, as the monkeys of the present triad had never been separated before (they were born and raised together in a domestic colony, and then housed together in the laboratory), they were thoroughly habituated to the testing environment and conditions, solitary testing included, prior to the present series of studies. As a result, they displayed the same modest plasma cortisol elevation (~ 10 $\mu\text{g}/\text{dL}$, a magnitude typical of mild stress in rhesus macaques; Rilling et al. 2001; Jahn et al. 2010; Raper et al. 2013) in both the Alone and

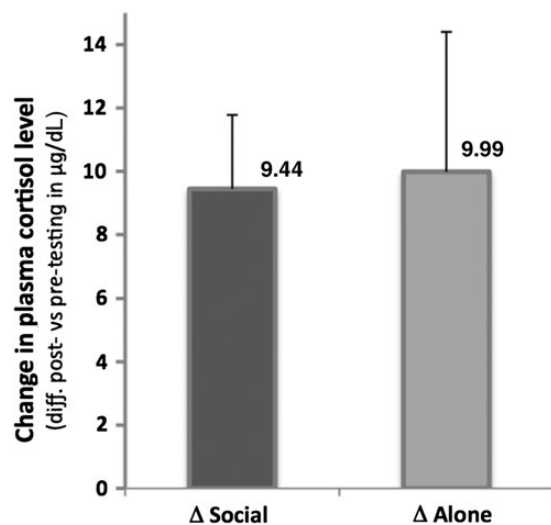
Social conditions. This excludes all stress-related phenomena, whether stress enhancing or stress buffering.

In his 1965 seminal paper, Zajonc hypothesized that cortisol, which he viewed as a physiological indicator of the subject's drive level, would be increased by the presence of a social other (Zajonc 1965). However, this hypothesis did not receive much attention in social facilitation research, and studies using other measures of physiological arousal (e.g., heart rate, skin conductance) generally failed to support this specific aspect of Zajonc's

Table 2 Left and right hand use in task-related behaviors during the FDG-PET sessions

	Right hand	Left hand
By monkey		
Monkey CE	1.5 ± 0.7	262.8 ± 111.4
Monkey CA	248.5 ± 131.9	30.4 ± 17.8
Monkey CI	91.5 ± 63.1	95.3 ± 52.8
Mean ± SEM	113.8 ± 50.9	129.5 ± 44.3
By condition		
Social	298.6 ± 132	340.9 ± 101.1
Alone	42.8 ± 36.5	47.5 ± 19.4

Note: Scores are seconds (mean ± SEM). By monkey—monkey CE was left-handed, monkey CA was right-handed and monkey CI was ambidextrous. At the group level, task-related hand use was equally distributed between the 2 hands. By condition—within each testing condition, task-related hand use was also equally distributed across the 2 hands. Social testing increased task-related hand use as expected, but there was no disproportionate increase in left-handed responses that could explain the right hemisphere lateralization of the accompanying neural changes.

**Figure 6.** Study III: cortisol assays. Testing induced the same modest elevation of plasma cortisol level in the present monkeys whether solitary or social.

theory. Furthermore, increased cortisol has more recently been associated with social isolation (rather than social presence), because it is a survival threat to social species (Hawkey et al. 2012). When it is supporting, social presence even dampens the hypothalamic-pituitary-adrenal axis (HPA) axis response to stressors (Hostinar et al. 2014). In monkeys, this social buffering of stress is characteristic of the mother-offspring relationship, but it can also occur among peers (Rilling et al. 2001). To date, it seems that the only situation reliably evoking the cortisol elevation expected by Zajonc is when social presence is coupled with a social threat, such as an explicit negative judgment in humans (Dickerson et al. 2008). Our own findings further dissociate social facilitation from stress by showing that performance enhancement can and do occur at the behavioral level without modification of the HPA axis response to stressors.

Social Facilitation: Monkeys Versus Humans

Monkey studies of social facilitation mostly focused on food simply made available for consumption (Visalberghi and Addessi

2000; Dindo and de Waal 2007; see Guerin 2009 for review). The present study adds to the rare evidence that monkeys are socially facilitated also when food serves as a reward for a task, whether motor (Dindo et al. 2009) or cognitive (Stamm 1961). Decades apart, the present results especially corroborate Stamm's (1961) observation that rhesus monkeys press a button to obtain food pellets about twice as more under social than under solitary testing. This comforts the idea that monkeys are good models to study the neuronal and psychophysiological bases of social facilitation.

Compared with humans, monkeys stand out, however, by the large effect size they display. Cohen's *ds* > 0.80 standard deviation unit, that is, denoting large effect sizes, are not unusual in monkeys. In rhesus macaques, the present data correspond to a *d* of 2.6, and Stamm's (1961) data to a *d* of 1.0. Likewise, in capuchins, the decreased latency to solve a novel foraging problem reported by Dindo et al. (2009) corresponds to a *d* of 1.3, and the increase in food consumption reported by Visalberghi and Addessi (2000) to a *d* of 1.1. Comparison of effect size across different dependent measures and different species must be taken with caution. Yet, it is worth noting that, in Bond and Titus's meta-analysis of 241 human studies of social facilitation, no *d*'s were larger than one-third of a standard deviation. In studies measuring response rate in simple tasks as we did here, *d* equaled 0.36 (Bond and Titus 1983, p. 276).

The causes of this difference in effect size are unknown. One possibility is that some social mechanisms are more influential in humans than in animals. For example, evaluation apprehension—the fear of others' disapproval—has a strong influence on human behavior. It seems to take another's presence plus the feeling of being evaluated for a marked social facilitation/inhibition effect to occur in humans (Feinberg and Aiello 2006). Another, nonexclusive possibility is that the 2 species are tested following different procedures. Animal studies typically rely on dyads, triads, or small troops of captive subjects tested with versus without their usual housemate(s). The present monkeys are a paradigmatic example as they have been tested with versus without the companions they have been living with since birth. Such level of intimacy is hardly reproducible in human studies, which most of the time use confederates unfamiliar to the subject as an audience. Familiarity is known for promoting social bonding and social learning (Monfardini et al. 2014). It has also been shown to enhance the audience effect on food consumption in humans, family, and friends, yielding greater social facilitation of food intake than other companions (de Castro 1994). It could likewise augment social facilitation of motor and cognitive performance.

Neural Markers of Social Facilitation

As emphasized in the Introduction, behavior alone cannot identify the mechanism mediating social facilitation, and the idea here was to gain novel insight based upon the brain changes associated with social facilitation. Specifically, we asked whether social facilitation, the performance enhancement brought by the mere presence of a social other, is accompanied by enhanced brain activity in the ventral brain network regulating motivation or in the dorsal brain network underlying attention. The imaging results failed to provide evidence supporting the idea that greater motivation (i.e., valuation of the reward) mediates the present social facilitation effect. Neither the whole-brain voxel-based analysis, nor the ROIs-based analysis revealed any significant changes in the major nodes of the brain reward circuit (Haber and Knutson 2010): the amygdala, orbital cortex, and ventral striatum.

Two brain networks showed greater activation for the Social than for the Alone condition, both located in the dorsal part of the brain. The first network was centered on primary cortices including the primary somatosensory area (SI) and the ventral part of the primary motor cortex (area F1; [Matelli et al. 1985](#)) and extending into the rostral inferior parietal lobule (area PF; [Pandya and Seltzer 1982](#)). In this network, the change was bilateral. Parietal area PF is predominantly connected with somatosensory motor areas SI, SII, PMv, and IPS ([Rozzi et al. 2006](#)) and plays an important role in organizing eating behavior, with neurons providing somatosensory information instrumental to the execution of food-related mouth motor acts ([Rozzi et al. 2008](#)). The ventral subdivision of area F1 is also involved in controlling goal-directed mouth motor acts ([Maranesi et al. 2012](#)). Consequently, the bilateral increase in activation of these 2 areas in the Social condition may be linked to the greater amount of task-related behaviors, especially mouth activity, associated with this condition.

The second network showing changes specific to social testing was the frontoparietal attention network. Increased activation concerned the IPFC (areas 45 and 46), the FEF, PMv (area F5; [Matelli et al. 1985](#)), the IPS, and the parietal area 5. Within this network, the most reliable (across analyses) and strongest (in magnitude and spatial extent) activation concerned the prefrontal cortex. Attention enables us to select some information for further processing, while setting aside other information ([Desimone and Duncan 1995](#)). In the brain, it is implemented by neurons that prioritize behaviorally relevant information over irrelevant distractors ([Ptak 2011](#)). Within the frontoparietal network, the prefrontal cortex is believed to be the crucial component for filtering distractors ([Suzuki and Gottlieb 2013](#)). Here, the frontoparietal network was already engaged in the Alone condition relative to the no-task baseline. The presence of a companion enhanced the task-driven activation seen in the Alone condition, especially in the prefrontal component of the network. This is as if, in line with the attentional theories of social facilitation (cf. Introduction, [Sanders and Baron 1975](#); [Baron 1986](#)), social presence intensified demands for stimuli prioritization and distractors filtering.

However counterintuitive, positive effects of distraction are well established in nonsocial contexts. Distracting subjects with easy secondary tasks or increasing their perceptual load improves attention focusing, decision-making, and memory in healthy humans ([Wierda et al. 2010](#)), as well as in patients suffering for attention ([Forster et al. 2014](#)) or memory ([Cashdollar et al. 2013](#)) disorders. For example, people distracted with music or word puzzles reach the best decision more often than people spending the same interval consciously thinking about the decision to be made ([Olivers and Nieuwenhuis 2005](#)). To interpret this growing body of data, [Lavie \(2010\)](#) proposed to distinguish perceptual load from cognitive control load and argues that attention focusing improves under high perceptual load (e.g., tasks involving many items or complex judgments) but deteriorates under high load on cognitive control processes (e.g., working memory). Tasks involving low perceptual load do not use up all attention resources, thus leaving spare capacity vulnerable to interference. In line with this modern variation of Baron's overload hypothesis, the presence of a social other facilitates low perceptual load tasks such as the present task by turning them into high perceptual load tasks.

Functional Asymmetry of the Changes in the Frontoparietal Attention Network

Lateralization of functions in rhesus macaques remains poorly understood making it difficult to interpret the functional

asymmetries revealed by monkey brain imaging in the present and other ([Blaizot et al. 2000](#); [Rilling et al. 2001](#)) studies. To date, it is generally accepted that macaques possess some equivalent of the human left hemisphere dominance for language and right hemisphere dominance for faces ([Hamilton and Vermeire 1988](#)), but it is not as yet accepted that they possess some equivalent of the human right hemisphere specialization in visuospatial attention ([Oleksiak et al. 2011](#)). Yet, monkeys with lesions limited to the right lateral prefrontal cortex do present attention disorders ([Rossi et al. 2009](#)) and resting state fMRI reveals lateralized, frontoparietal, intrinsic functional connectivity networks in awake monkeys ([Hadj-Bouziane et al. 2014](#); [Wey et al. 2013](#)). Because the attention regions presenting a right lateralization here, the IPFC, FEF, and PMv, also contribute to hand and eye movements ([Simon et al. 2002](#)), and because social facilitation, by definition, increases task-related responses, a motor explanation had to be considered. We found no disproportional increase of left-handed responses during social testing (compared with the Alone condition) that could explain a predominantly right change in brain activity. We could not quantify eye movements in the present freely moving animals but the possibility of a specific increase of leftward saccades during social testing seems farfetched. Since social testing increased both right and left hand use as well as mouth use, bilateral changes seen in primary cortical areas SI and F1 appear more likely to reflect motor-related changes, and IPFC, FEF, and PMv, lateralized, attention-related changes. There is no social facilitation neuroimaging study in humans to compare the present findings with, but a study exploring the neural impact of a social presence that did not affect behavior ([Nawa et al. 2008](#)) did report a lateralized, right IPFC activation.

Generalizability of the Present Findings: a Challenge for the Future

In 2008, Wagstaff and colleagues proposed the first neuropsychological model of social facilitation (hypothesizing that the presence of others facilitates tasks dependent on posterior brain regions and inhibits tasks dependent on the frontal cortex; [Wagstaff et al. 2008](#)). However, no prior animal or human study has actually investigated the neural substrates of a performance enhancement induced by the mere presence of a peer. The present study is therefore a first step. It demonstrated that task-related activity in nonfood-deprived animals, used to the mild stress of testing, and performing the simple task of touching images to obtain food treats, was higher when the animals were tested with a lifetime companion compared with when tested alone. The increase concerned the primary somatosensory and motor cortex bilaterally, and the frontoparietal attention network unilaterally. This proves the neural validity of the attentional theory of social facilitation. It does not disprove, however, the neural validity of the motivational or any other theory. As the various theories of social facilitation are not mutually exclusive, there could be elements of each occurring in any particular situation.

Future studies will need to determine whether social facilitation systematically relies on the attention network whatever the companion (familiar, unknown, neutral, supporting, threatening) and the behavior (food consumption, decision making, habit learning, declarative memory, etc.) or, alternatively, simply enhances activity in whatever brain substrate supports the task at hand in the species under consideration. The latter hypothesis has the advantage to provide a parsimonious explanation for the widespread phylogenetic representation of social facilitation, one that could hold from primates, human, and nonhuman to birds and insects.

Supplementary Material

Supplementary material can be found at: <http://www.cercor.oxfordjournals.org/>

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