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Altered Communicative Decisions following Ventromedial Prefrontal Lesions

Highlights

- Patients with vmPFC damage are able to select communicatively effective behaviors
- However, their communicative decisions are not tuned to knowledge about a social partner

Authors

Arjen Stolk, Daniela D'Imperio, Giuseppe di Pellegrino, Ivan Toni

Correspondence

arjen.stolk@donders.ru.nl

In Brief

Stolk et al. demonstrate that patients with damage to the ventromedial prefrontal cortex are able and motivated to select communicatively effective behaviors during social interaction. Yet, their communicative decisions are not fine-tuned with their knowledge of a social partner, namely, knowledge based on prior stereotypes and ongoing behaviors.

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Altered Communicative Decisions following Ventromedial Prefrontal Lesions

Arjen Stolk,[1,*] Daniela D'Imperio,[2,3,4] Giuseppe di Pellegrino,[2,3] and Ivan Toni[1]
[1]Donders Institute for Brain, Cognition, and Behaviour, Radboud University, 6500 HB Nijmegen, the Netherlands
[2]Centre for Studies and Research in Cognitive Neuroscience, 47023 Cesena, Italy
[3]Department of Psychology, University of Bologna, 40127 Bologna, Italy
[4]Department of Psychology, Sapienza University of Rome, 00185 Rome, Italy
*Correspondence: arjen.stolk@donders.ru.nl
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SUMMARY

Damage to the human ventromedial prefrontal cortex (vmPFC) leads to profound changes in everyday social interactions [1, 2]. Yet, in the lab, vmPFC patients show surprising proficiency in reasoning about other agents [3–8]. These conflicting observations suggest that what vmPFC patients lack in everyday social interactions might be the ability to guide their decisions with knowledge about a social partner [9–13], despite preserved access to that knowledge [2, 14]. Quantification of socially relevant decisions during live interaction with different partners offers the possibility of testing this hypothesis. Eight patients with vmPFC damage, eight patients with brain damage elsewhere, and 15 healthy participants were asked to communicate non-verbally with two different addressees, an adult or a child, in an experimentally controlled interactive setting [15, 16]. In reality, a confederate blindly performed the role of both adult and child addressee, with matched performance and response times, such that the two addressees differed only in terms of the communicator's beliefs. Patients with vmPFC damage were able—and motivated—to generate communicatively effective behaviors. However, unlike patient and healthy controls, vmPFC patients failed to adjust their communicative decisions to the presumed abilities of their addressee. These findings indicate that the human vmPFC is necessarily involved in social interactions, insofar as those interactions need to be tailored toward knowledge about a social partner. In this perspective, the known contribution of this region to disparate domains like value-based decision-making [17–19], schema-based memory-processing [20–22], and person-specific mentalizing [11–13] might be instances of decisions based on contingently updated conceptual knowledge.

RESULTS

Everyday social interactions often require acting on social stimuli according to rules made cognitively opaque by their reliance on knowledge implied in the circumstances of an interaction and presumed to be commonly known [23, 24]. For instance, communicating even a simple spatial location relies on generating a response from an open-ended set of possibilities, on the basis of a conceptual space continuously updated with knowledge idiosyncratically shared across communicators [25–29]. In contrast, laboratory tests of social functioning often require binary decisions in situations that can be solved deductively (e.g., the Sally-Anne task [30]). Patients with ventromedial prefrontal lesions can deal with the latter, but not with the former [1–8], suggesting a dissociation between a preserved ability to make logical decisions involving other cognitive agents and an impaired ability to tune those decisions with implied knowledge about those agents.

We tested for this dissociation by assessing whether a focal lesion to the human ventromedial prefrontal cortex (vmPFC) interferes with adjusting decisions according to implied knowledge about addressees of a communicative interaction, while preserving the ability to take effective communicative decisions. Those decisions were quantified during live non-verbal interactions between a communicator (the participant) and an addressee (a confederate) on a digital game board (Figure 1A; Movie S1). On each trial, their joint goal was to collect an object from the game board. Only the communicator knew the object location, and only the addressee could collect the object, leading the communicator to select behaviors that the addressee could interpret for understanding where the object was located. These circumstances drive communicators and addressees to converge on a limited but idiosyncratic number of strategies from an open-ended set of possibilities, such that different pairs use different communicative strategies to convey the same meaning [26, 27]. The crucial experimental manipulation quantified alterations in communicative behaviors driven by implied knowledge about the addressee, other factors being kept equal. Namely, each participant was informed that he would be playing the communicative game with two different addressees, either an adult or a child, sitting in separate rooms with their own monitors to see the communicator's token moving on the game board. In reality, a confederate blindly performed the role of both adult and child addressee, with matched performance and response times ($F < 0.4$; see the Supplemental Results), such that the two addressees differed only in terms of the communicator's beliefs (Figure 1A).

Previous work shows that communicators' beliefs about the age of their interlocutor influences their communicative decisions during both naturalistic and experimentally controlled

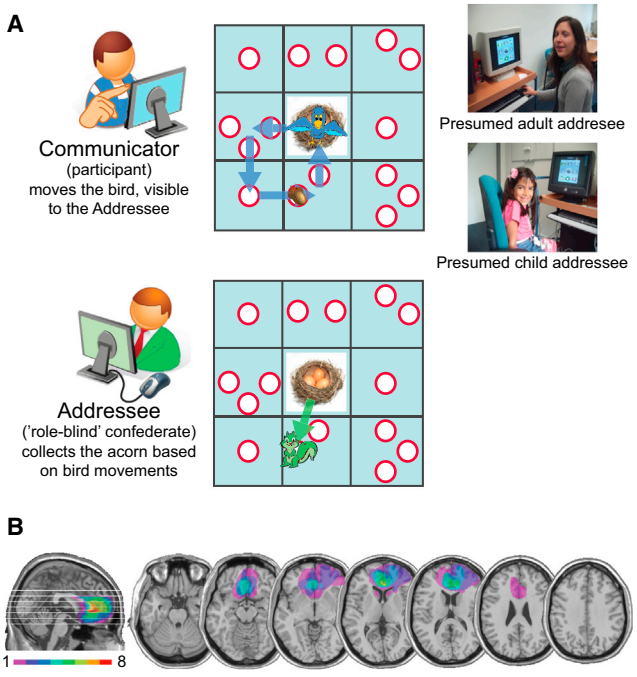

Figure 1. Communication Task and Brain Lesion Overlap

(A) The joint goal of the communicator and addressee is to collect an acorn from the digital game board. Knowledge of the acorn's location in the game board is available to the communicator only (the bottom-middle square in this particular example). However, only the addressee can collect the acorn. This situation leads the communicator to inform the addressee, by virtue of movements of a bird on the game board, where the acorn is located. At trial onset the bird token is positioned on the central square of the game board (nest), where it needs to be returned to signal the end of the movement epoch. By touching a square on the screen with his/her finger, the communicator can move the bird to that square, and this movement is also visible to the addressee. However, the bird can only move to the center of each of the nine grid squares, and only through vertical or horizontal displacements (Movie S1). This feature of the task makes it difficult for the communicator and the addressee to disambiguate the location of multiple potential targets within a square (the white circles) on the basis of the location of the bird alone. In contrast to the communicator, the addressee has no spatial restrictions on the movements of the squirrel on the game board. Participants were informed that they would be playing the game, as communicators, with another adult and with a 5-year-old child, in alternation. A digital photograph of the current presumed addressee was presented to the communicator in full screen before the onset of each block of five trials and in the top-right corner of the screen during each block. In reality, a confederate performed the role of both addressees, while remaining blind to which one of the two roles he was performing in any given trial.

(B) Location and degree of overlap of brain lesion in eight patients with vmPFC damage. The color bar indicates the number of overlapping lesions. Maximal overlap occurs in Brodmann areas 10, 11, and 32.

See also Table S1 and Movie S1.

interactions, resulting in stronger emphasis on communicatively relevant portions of utterances directed to a child [15, 16, 31–33]. For instance, the communicative game used in this study has repeatedly shown that participants spontaneously generate communicatively specific adjustments toward a younger addressee, spending longer time on the location of the target object, but not on other board locations [15, 16]. This experiment exploits those communicative adjustments as a quantitative marker of implied knowledge about other agents during socially relevant decisions, in the context of a production task simple enough to be performed reliably without training even by pediatric and brain-lesioned populations [16, 34].

Eight patients with vmPFC damage (Figure 1B), eight patients with brain damage elsewhere, and 15 healthy controls were compared on task performance, with "voxel-based lesion-symptom mapping" (VLSM) providing a data-driven index of the relationship between lesion location and communicative performance [35]. vmPFC patients' decisions (66% ± 12% success rate, mean ± SD) were well above chance level (6.7%; 15 potential object locations in any given trial) and as communicatively effective as those made by the brain-damaged and healthy control groups (55% ± 26% and 59% ± 21%, respectively; $p > 0.29$). For instance, both vmPFC and control groups used time as a tool to put emphasis on communicatively relevant locations of the game board (Figure S1). The three groups differed in terms of the magnitude of communicative adjustment made to the presumed abilities of the addressees ($F(2,28) = 5.2$, $p = 0.012$, effect size partial $\eta^2 = 0.27$). Namely, the vmPFC patients had smaller communicative adjustment than the lesion and healthy control groups ($p = 0.006$ and $p = 0.011$, respectively; vmPFC, $t(7) = -1.6$, $p = 0.17$; lesion controls, $t(7) = 4.5$, $p = 0.003$; healthy controls, $t(14) = 2.3$, $p = 0.040$; Figure 2A). An independent VLSM analysis of the lesion-behavior relationship confirmed that intact tissue in the ventromedial sector of the frontal lobes is relevant for tailoring communicative decisions toward the presumed abilities of an addressee ($Z = 3.4$, $p = 0.0007$; Figure 2C).

Two additional observations indicate that the failure of vmPFC patients to tune their communicative behavior to other agents was not due to motivational or perseveration problems. First, vmPFC patients spent disproportionally more time than patient and healthy controls on communicatively relevant portions of the game board, independently from time spent elsewhere on the game board ($F(2,27) = 3.5$, $p = 0.045$; vmPFC versus lesion controls, $p = 0.029$; vmPFC versus healthy controls, $p = 0.019$; Figure S1). This means that vmPFC patients made more emphatic communicative movements than required, violating the Gricean communicative maxim of quantity [37], but showing that they were willing to invest resources in switching between communicative and instrumental portions of their actions and in marking a communicatively relevant location for the benefit of the addressee (e.g., Movie S1). Second, after a misunderstanding, vmPFC patients did not increase the temporal contrast between communicative and instrumental components of their behaviors, as observed in lesion and healthy control groups (vmPFC versus lesion controls, $U(12) = 4$, $p = 0.010$; vmPFC versus healthy controls, $U(21) = 26$, $p = 0.028$; Figure 2B; Movie S2). Yet, vmPFC patients moved systematically longer after an error than after a correct trial ($t(7) = 3.1$, $p = 0.018$), excluding the possibility that the lack of error-related communicative adjustments was due to a failure to detect or to react to the discrepancy between the expected and observed behavior of the addressee.

DISCUSSION

This study quantified the consequences of a lesion to the human vmPFC during live communicative interactions, providing

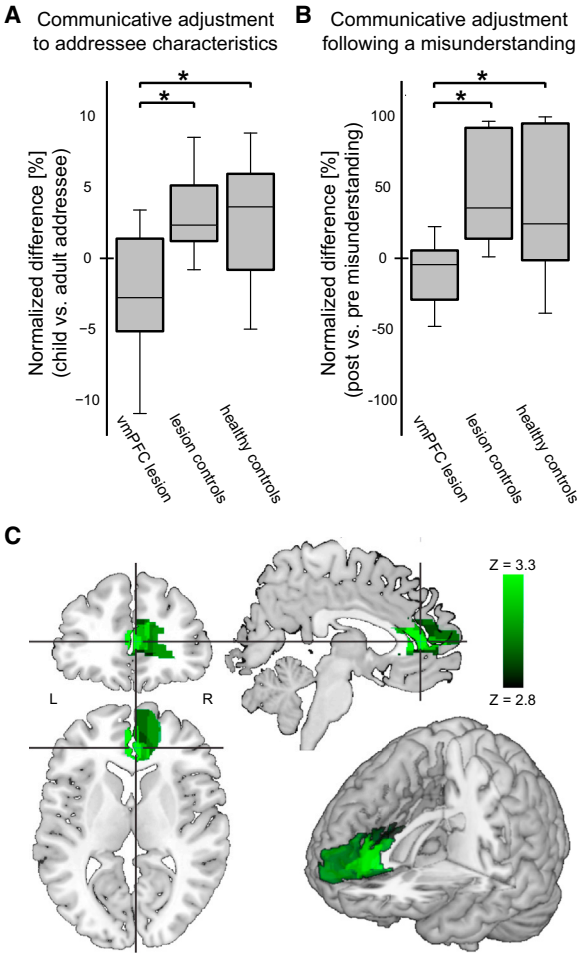

Figure 2. Communicative Adjustments and Voxelwise Relevance of Lesion Site

(A) Communicative adjustments to the presumed characteristics of the addressee. In this plot, communicative adjustments are indexed as the normalized difference of time spent on the location where the acorn was located between presumed child and adult addressees ([child − adult] / [child + adult]), separately per participant group (vmPFC, lesion controls, and healthy controls). The central mark is the median, the edges of the box are the 25th and 75th percentiles, and the whiskers illustrate the data range (besides outliers).

(B) Communicative adjustments to a misunderstanding. In this plot, communicative adjustments are indexed as the relative difference between time spent on the location where the acorn was located and the board locations visited during a trial. The effect is between the trial after a misunderstanding and the preceding trial ([$trial_t$ − $trial_{t-1}$] / [$trial_t$ + $trial_{t-1}$]).

(C) Analysis of the relationship between brain lesion and communicative adjustment reveals voxelwise relevance for adjusting communicative decisions to the presumed abilities of the addressee. For each voxel, participants spared from a lesion to that voxel were selected from the entire sample population, and their communicative adjustments were compared against a null distribution of no adjustment. The threshold of the color axis was adjusted to resolve the spatial structure around the statistically significant peaks: z values correspond to $0.005 > p > 0.001$ (two-tailed). Peak voxels centered on MNI (Montreal Neurological Institute) coordinates [4, 9, 36], falling into Brodmann area 32 extending into area 10.

*$p < 0.05$. See also Figure S1 and Movies S2 and S3.

evidence that this cortical structure is necessary for adjusting decisions to implied knowledge about a social partner. Patients with damage to the vmPFC communicated as effectively as patient and healthy control groups, using time as a tool to put emphasis on communicatively relevant locations of the game board, a behavior functionally equivalent to the use of prosodic markers during verbal communication [24, 31]. The crucial finding is that vmPFC patients spent disproportionally longer time on those locations, irrespectively of the presumed characteristics of the addressee, whereas the control groups fine-tuned their communicative decisions to implied knowledge about the addressee. Furthermore, after a misunderstanding, the vmPFC patients failed to increase the contrast between communicative and instrumental components of their behaviors [25], despite the incentive to adjust their behavior. These findings extend recent observations on the decision-related dynamics of this region during interpersonal communication [26], suggesting that the human vmPFC is necessary for guiding decisions with knowledge about a social partner, as inferred from prior stereotypes and ongoing behaviors [9–11].

This selective communicative deficit recapitulates the proficiency of vmPFC patients in laboratory tests of social functioning [3–8] and their impairments in situations requiring decisions based on implied social knowledge [1, 2, 38–40]. For instance, vmPFC patients might disclose intimate personal information to an interviewer they have just met [2], fail tests that probe humor interpretation and social expectations [6, 39], or accept socially unfair financial offers [40]. Yet, those patients can reason about the mental states of other agents, when those inferences do not need to be fine-tuned with background information about those agents [3–8]. Healthy individuals use vmPFC when mental state reasoning requires access to this implied knowledge, for instance to make inferences about the idiosyncratic mental states of specific individuals [12, 13, 36, 41]. The pattern of proficiency and deficits observed across those studies and in this work can be explained by considering a dissociation between a vmPFC-independent ability to select socially effective behaviors and a vmPFC-dependent ability to adjust those decisions with implied knowledge about other agents. The crucial deficit appears to lie in the ability to use social knowledge for fine-tuning decisions, rather than for making complex decisions or retrieving social knowledge [2, 14, 42]. For instance, vmPFC patients have verbal access to the concept of gender, but that knowledge is not automatically taken into account during speeded decisions [14]. Similarly, in this study, the vmPFC group accurately rated the addressees' ages (6 ± 1 and 21 ± 7 years for child and adult, respectively; mean ± SD), but it did not use that knowledge to adjust communicative behavior. Access to implied knowledge for fine-tuning a behavior is particularly relevant during social decisions, but it is also used in other situations in which choices from a large set of possibilities are facilitated by embedding those possibilities within pre-existing knowledge schemas [20–22]. Accordingly, vmPFC patients seem to be immune to false-recall effects during linguistic processing, driven by automatic embedding of semantic items within existing schematic knowledge [21]. This interpretation of vmPFC function suggests that the contribution of this region to value-based decisions [17–19] can be seen as an instance of its general role in adjusting decisions according to continuously updated schemas for navigating

the search space of possibilities [43]. By the same token, the association of this region with processing others' emotions [4, 8, 44] might be a function of tasks requiring contingent updating of agent-specific knowledge, rather than emotional material per se.

This interpretation of vmPFC function is well grounded in the connectivity profile of this region. On the one hand, the rostral portion of this region (medial area 10) is robustly connected with cingulate motor areas [45] and with the head of the caudate [46], making it possible for the vmPFC to influence the computation of action values according to a model of their long-term expected consequences [18, 19]. On the other hand, both rostral and perigenual portions of the vmPFC (medial areas 10 and 32, respectively) have strong reciprocal connections with the anterior part of the superior and medial temporal lobe [45, 47–49], making it possible for the vmPFC to access knowledge schemas dynamically adjusted to an ongoing social interaction [26, 27]. This connectivity profile endows the human vmPFC with the ability to guide decisions with social knowledge abstracted from prior stereotypes and continuously updated with ongoing behavior, a capacity arguably necessary for navigating through an ambiguous and fleeting social world [10, 50].

Methodological Considerations

It might be argued that the communicative setting used here is a simplistic approximation of the complexity intrinsic in everyday social interactions or in experimentally controlled decision-making protocols [26, 42]. Actually, the current task requires the generation of communicative behaviors from an open-ended set of possibilities, continuously updated with the shared knowledge of the communicators [27]. These computational challenges are well beyond the binary choices typically required during lab-based tests of decision-making.

The communicative adjustments reported here might appear cognitively crude and numerically tenuous, and it might be argued that large communicative adjustments would be more relevant. In fact, overly exaggerated displays would make them more informative than required, violating communicative principles [37]. Accordingly, the subtle spontaneous adjustments captured in this study are directly linked to daily communicative abilities, quantifying the same cognitive capacity that leads adults to modify their speech, gestures, and body motions when addressing a child [31–33]. Furthermore, those spontaneous adjustments are reliable [15, 16] and have a temporal precision more likely to reflect implicit knowledge than explicitly designed strategies (e.g., Movie S3). Accordingly, those adjustments provide the opportunity to compare decisions across groups that might have different strategic biases and levels of motoric performance.

The precise anatomical location and demarcation of the vmPFC varies across research fields. For instance, in the decision-making literature, vmPFC often refers to a swathe of tissue closer to the orbital surface (medial areas 11 and 14) [17]. The cortex corresponding to the lesion site reported here has also been labeled as rostroventral dorsomedial PFC [51]. Furthermore, recent work indicates that orbital and rostral/perigenual portions of the vmPFC may differ in terms of their resting state connectivity profile [47]. Unfortunately, those fine-grained parcellations and labeling schemes go beyond the resolution afforded by lesion-symptom mapping following vascular pathology [52]. For instance, in this study, consistent but erroneous lesion-symptom association may have occurred in the vicinity of the anterior cerebral artery and its branches, requiring caution when scrutinizing the VLSM result. Studying the consequences of smaller cortical lesions not directly linked to the vascular architecture (e.g., after surgical resections) might allow one to resolve whether and how these vmPFC portions may differ in their contributions to human social decisions.

Conclusions

Damage to the human vmPFC leads to profound changes in everyday social interactions [1, 2]. By quantifying interpersonal communication, we show that patients with lesions in that cortical region are still motivated and able to communicate effectively but fail to adjust their communicative decisions to the presumed abilities of the addressee. These findings indicate that the human vmPFC is necessarily involved in social interactions, insofar as those interactions need to be guided with knowledge about an individual social partner. This conceptualization of vmPFC function unifies disparate observations from value-based decision-making [17–19], schema-based memory-processing [20–22], and mentalizing phenomena [11–13], offering a new window into the cognitive alterations observed in disorders like frontotemporal dementia and autism spectrum disorders [7].

EXPERIMENTAL PROCEDURES

The experimental procedures are summarized briefly throughout the Results and are presented in complete detail in the Supplemental Experimental Procedures.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Results, Supplemental Experimental Procedures, one figure, one table, and three movies and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.03.057.

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