# Neural mechanisms of communicative innovation

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**Human referential communication is often thought as coding–decoding a set of symbols, neglecting that establishing shared meanings requires a computational mechanism powerful enough to mutually negotiate them. Sharing the meaning of a novel symbol might rely on similar conceptual inferences across communicators or on statistical similarities in their sensorimotor behaviors. Using magnetoencephalography, we assess spectral, temporal, and spatial characteristics of neural activity evoked when people generate and understand novel shared symbols during live communicative interactions. Solving those communicative problems induced comparable changes in the spectral profile of neural activity of both communicators and addressees. This shared neuronal up-regulation was spatially localized to the right temporal lobe and the ventromedial prefrontal cortex and emerged already before the occurrence of a specific communicative problem. Communicative innovation relies on neuronal computations that are shared across generating and understanding novel shared symbols, operating over temporal scales independent from transient sensorimotor behavior.**

social interaction | theory of mind | experimental semiotics | MEG | broadband spectral change

We can modify reality by selecting either instrumental actions that change the physical state of the environment according to the mechanics of the action or communicative actions that change the mental state of other agents according to the content of the action (1, 2). For instance, we can fill a glass with a drink or ask a bartender to do that. A common language might help to achieve the latter by providing access to previously established shared symbols, but those symbols presuppose a computational mechanism powerful enough to negotiate them across interlocutors (3). Here, we study the electrophysiological correlates supporting the rapid negotiation of shared symbols, a fundamental property of human communication (4, 5).

Given the vast number of possible meanings that can be attributed to a novel communicative action (6, 7), it remains unclear how novel shared symbols can be rapidly selected and understood. General-purpose learning algorithms such as temporal difference or Hebbian learning (8, 9) do not seem suitable, because they require many trials to converge on statistically relevant features. There are brain circuits that support fast predictions on sensory inputs or consequences of planned actions (10, 11), but those circuits are geared toward a specific domain of application with well-defined priors [e.g., faces (12)]. Novel shared symbols, being novel, do not have well-defined priors (3, 13, 14). Solving this type of communicative problem requires a mechanism that supports a rapid exploration through a large search space, generating connections between different conceptual structures (15, 16).

These theoretical considerations about human communication lead to three predictions on its underlying mechanism. First, given that establishing shared symbols requires taking into account the inferred knowledge of the interlocutor ["audience design" (17–19)], the generation and comprehension of those symbols should involve neural patterns associated with flexible conceptual knowledge (20–23), rather than sensorimotor couplings with limited generalization patterns (9, 24–28). Second, cerebral activities supporting these conceptual processes during generation and comprehension of novel shared symbols should overlap, given that these processes relate to the specific conversational context shared by the interlocutors of the communicative exchange (29). Third, cerebral activity supporting this predicted overlap should predate in time the processing of the communicative stimuli themselves, given that the meaning of any stimulus arises from a conceptual space defined by the ongoing communicative interaction (19, 30), rather than by the sensory material itself.

We test these predictions by characterizing spatial, spectral, and temporal features of neural activity supporting the planning and understanding of novel communicative actions, using an absolute index of source-reconstructed magnetoencephalographic activity. In contrast to previous work largely focused on individuals perceiving instrumental actions (31, 32) or known linguistic material (30, 33), here we investigated both production and comprehension of novel communicative actions during a live interaction between pairs of participants and directly contrast those phenomena with a control interaction involving no communicative necessities (Fig. 1).

## Results

**Task Manipulation.** We studied 24 pairs of participants engaged in real-time controlled interactions (18) and measured neural activity with magnetoencephalography (MEG) from one participant within each pair. Each pair of participants played an interactive game that requires the generation and understanding of novel, mutually negotiated communicative actions (i.e., communicative interactions between a "Communicator" and an "Addressee" pair; Fig. 1 and Movie S1). We distinguished neural activity specifically associated with those communicative actions from activity evoked during another interactive game that involved the same stimuli, responses, attention, and between-participant dependencies but no communicative necessities (i.e., instrumental interactions between a "Salesman" and a "Roadworker" pair; Fig. 1 and Movie S2). Within each task, participants alternated between those two task-specific roles on a trial-by-trial basis (80 trials in each task). We further distinguished neural activity common to both generating (epoch D: planning; Fig. 1) and understanding communicative actions (epoch E: observation; Fig. 1) from activity uniquely evoked by either task component by means of conjunction analyses (34). An absolute index of neural activity was quantified by estimating ("beamforming") time-resolved spectral power of the signals recorded with MEG before and during task performance (35).

The communicative and instrumental tasks are explained in detail in *SI Materials and Methods*. Here, we highlight their overlapping and differing features relevant for labeling and

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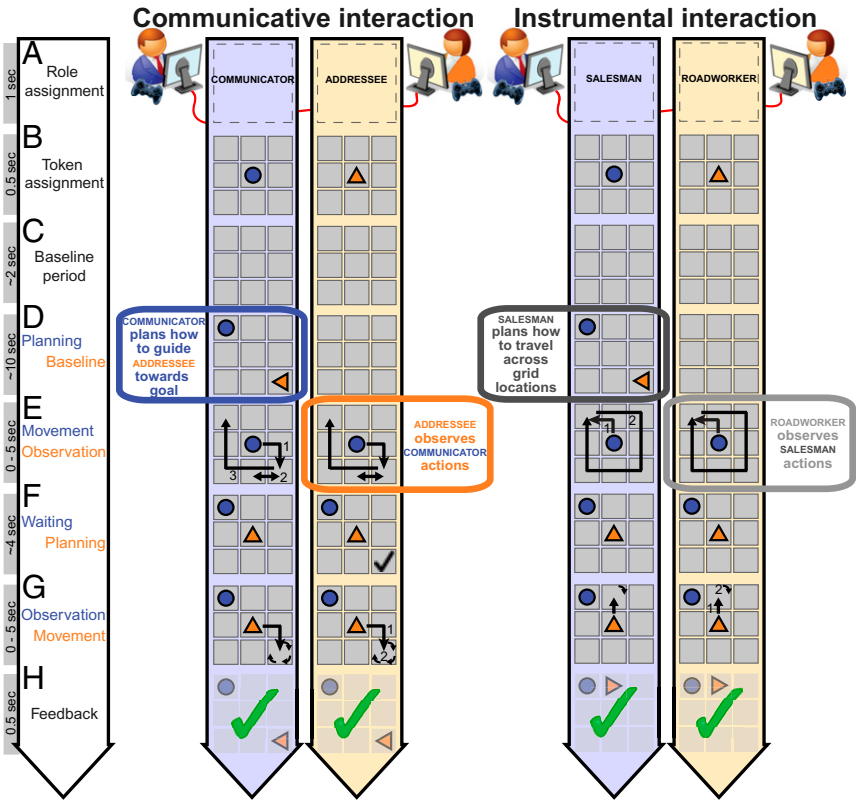


**Fig. 1.** Live interactions. During a communicative interaction (Movie S1), pairs of participants had to jointly reproduce a spatial configuration of two tokens shown only to the Communicator (epoch D). This required the Communicator to use the movements of his token (in blue) (epoch E) to indicate to the Addressee how she should configure her token (in orange). In this game, shared meanings of the behaviors had to be constructed and inferred. During an instrumental interaction (Movie S2), the same pair interacted by moving their tokens on the board according to preassigned rules. The Salesman implemented his rules on a visually presented configuration. The Roadworker implemented her rules according to the behavior of the Salesman in epoch E. The critical epochs for the analysis of neural activity are the planning phase (epoch D) for the Communicator/Salesman and the observation phase (epoch E) for the Addressee/Roadworker.

interpreting the results. In both tasks, pairs of participants were instructed to move their token on a visually presented 3 × 3 digital grid (Fig. 1). In the communicative task, the goal of the Communicator was to make sure that both his token (e.g., a circle) and that of the Addressee (e.g., a triangle) were arranged according to a configuration visually presented to the Communicator only. This required the Communicator to use the movements of his token to indicate to the Addressee how she should configure her token on the grid. This task has proven effective in encouraging the generation of pair-specific communicative behaviors (18, 36, 37). The same movements could be used by different pairs to negotiate different meanings, and the same meaning could be conveyed by different movements across different pairs (Movie S3). The same movement could even be used to convey different goal states by the same pair in different trials (Movie S4) and vice versa (Movie S5). The latter observation emphasizes how, in this game, a movement acquires meaning by virtue of the history of the communicative interactions within a given pair, rather than by virtue of its sensory attributes. In the instrumental task, the goal of the Salesman was to move his token across the board following a learned rule, according to a visually presented configuration. The coplayer, labeled Roadworker, was instructed to place her token on the board following a learned rule, according to the movements of the Salesman on the board. Stimuli, movements, and between-player dependencies were matched between the two types of interactions, but the necessity to construct and infer shared movement-meaning mappings differed. In the communicative task, the success of a trial relied on the Communicator designing an action that can be understood by the Addressee, and on the Addressee inferring the Communicator's intentions. In the instrumental task, the success of a trial relied on each of the two players implementing preestablished rules, without communicative requirements, despite the fact that the actions of the Roadworker were determined by those of the Salesman.

**Behavioral Characteristics of Communicative Interactions.** Participants solved both tasks well above chance level (communicative trials: 71 ± 3% correct; instrumental trials: 73 ± 4% correct; mean ± SEM; Fig. S1*E*; estimate of chance level: 1/32th; eight locations with four potential orientations). The communicative interactions evoked stronger mutual adjustments between pairs than the instrumental interactions. First, during the communicative interactions, Communicators spent longer times at the grid location where the Addressee should place her token (Addressee "target"), compared with other visited locations on the board ["nontargets"; location × task interaction: $F(1,23) = 108.0$, $P < 0.001$; Fig. S1*F*]. This pausing behavior was adjusted to the inferred knowledge of the communicative partner on a trial-by-trial basis (36), a quantitative indication of recipient design (38). Second, during the communicative interactions, Communicators made repeated movements from and to the target location to indicate the desired orientation of the Addressee's token (2.09 ± 0.49 visits per trial; mean ± SD; see action 2, epoch E in Fig. 1, communicative task). This behavior was not observed in the instrumental task, and it follows the general principle of using a patently dysfunctional action to ostensively mark the action as being communicative in nature (14). Third, in the communicative interactions, the within-trial coupling between Communicator and Addressee planning times ($r = 0.29 \pm 0.17$; $z$-transformed cross-correlations) was stronger than in the instrumental interactions [i.e., between Salesman and Roadworker planning times; $r = 0.09 \pm 0.22$; $t(23) = 4.2$; $P < 0.001$]. This observation suggests that a difficult communicative problem was concomitantly more difficult for both Communicators and Addressees (18, 39). Fourth, in the instrumental task, the number of executed movements explained a larger portion of planning time variance than in the communicative task [instrumental: $r = 0.63 \pm 0.12$; communicative: $r = 0.42 \pm 0.17$; $t(23) = 5.5$, $P < 0.001$]. This finding suggests that, in the instrumental task, planning times increase almost linearly with an increasing number of movement steps to plan. In contrast, in the communicative task, planning times were governed

by cognitive operations less directly related to the mechanics of the individual movement steps.

**Neural Characteristics of Communicative Interactions: Spatial and Spectral Features.** Having shown the relevance of the communicative task for studying novel communicative actions, we also verified that the neural activity evoked by performance of the communicative and instrumental tasks was largely matched (Fig. S2) and devoid of eye-movement confounds (Fig. S3). Having satisfied these preconditions, we proceeded to test the three hypotheses of this study. First, we isolated neural activity evoked by the communicative task over and above the instrumental task, testing whether those neural differences were present in the sensorimotor system or in higher-order cortical areas. We considered the whole time interval covered by the planning and observation epochs (epochs D and E in Fig. 1), a conservative approach that intrinsically focuses toward neural effects spanning both epochs. Two brain regions [right temporal lobe (TL) and ventromedial prefrontal cortex (vmPFC); Fig. 2 *A* and *C*] falling outside the core sensorimotor systems exhibited significantly stronger power over a broad frequency range (Fig. 2 *B* and *D*) during the processing of communicative actions than during instrumental actions. There were no significant clusters where planning or observing instrumental actions evoked stronger responses than communicative actions.

The second hypothesis of this study predicts an overlap in the cognitive processes evoked during generation and comprehension of novel shared symbols. Accordingly, we tested whether those task-dependent neural differences are shared between planning (epoch D) and observing (epoch E) communicative actions. We used a minimum-statistic conjunction analysis (34) to isolate neural effects shared across communicative roles, and different from the corresponding instrumental roles (40), effectively filtering out between-tasks differences that are not consistent across paired roles within each task (Fig. S1 *C* and *D*). The overlap in neural effects across communicative roles was statistically most pronounced in the 55–85 Hz γ-band (Fig. S4) and spatially encompassed the vmPFC and the right TL (Fig. 2*E*, in brown).

**Neural Characteristics of Communicative Interactions: Temporal Features.** The third hypothesis of this study predicts that selecting and understanding novel shared symbols relies on a cognitive set implemented through ongoing neural activity that predates the occurrence of the communicative stimulus material itself. Therefore, we explored the temporal dynamics of an absolute index of neural activity [i.e., source-reconstructed time-resolved estimates of γ-band power (35)]. This index is appropriate for isolating tonic state-dependent effects that are temporally stable and not exclusively bound to the occurrence of task events. We observed up-regulated neural activity in three regions (Fig. 3). A ventrolateral portion of the right TL showed a tonic up-regulation of γ-band power during both planning and observation of communicative actions (TL; Fig. 3 *A* and *B*), without transient responses time-locked to the sensorimotor events occurring during those epochs. This temporal dynamics indicate that neural activity in the right TL is modulated by the communicative task but over a timescale decoupled from within-trial events. A different neural dynamics was found in the vmPFC. This region showed a sustained decrease in γ-band power during the observation epochs of both tasks, again with stronger γ-band power in the communicative task, and a sharp power increase when participants started selecting their actions on the basis of the observed movements of their coplayer (vmPFC; Fig. 3). These temporal

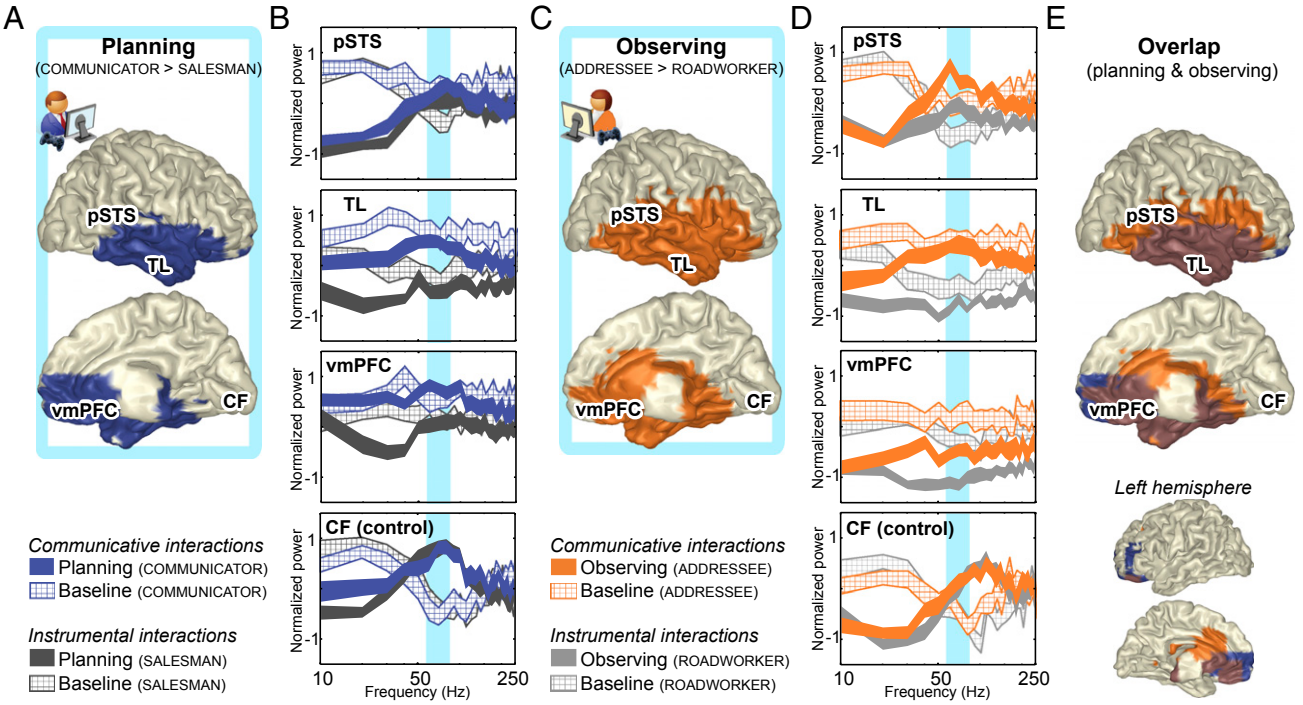


**Fig. 2.** Spatial and spectral characteristics of neural activity evoked during communicative and instrumental interactions. Brain regions exhibiting stronger γ-band activity (55–85 Hz) when participants planned (*A*) and observed (*C*) communicative actions compared with instrumental actions. The spatial distribution of the conjunction (in brown) (*E*) was lateralized to the right hemisphere, covering most of the TL and vmPFC. Power spectral densities of neural activity (±1 SEM, striped for baseline epochs, filled for task epochs) (*B* and *D*) indicate that the task differences were broadband in nature (compare blue vs. dark gray and orange vs. light gray ribbons), statistically most pronounced in the 55- to 85-Hz frequency range (in cyan). Spectral power is mean-centered (i.e., the average across the eight experimental epochs was set to zero) and variance-normalized (SD = 1) over subsequent 10-Hz frequency bins. When averaged over the whole task epochs, the differences in the right pSTS were present only during the observation epoch (but see Fig. 3). The CF is presented for control purposes, showing only band-limited modulations from baseline.

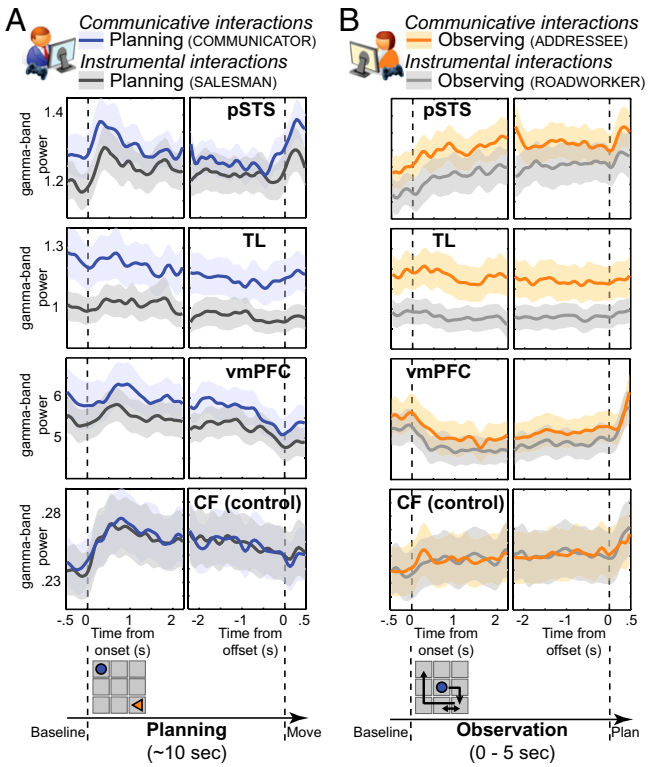


**Fig. 3.** Temporal characteristics of neural activity evoked during communicative and instrumental interactions. γ-Band activity (55–85 Hz; in arbitrary units ± 1 SEM) in pSTS, TL, vmPFC, and CF, time-locked to planning (*A*) and observation (*B*) onset and offset. The graphic panel at the bottom highlights the characteristics of the relevant task epochs. Both tasks induced transient changes in neural activity in pSTS, vmPFC, and CF. During the communicative task, neural activity was tonically up-regulated in TL, vmPFC, and pSTS but not in CF.

dynamics indicate that neural activity in the vmPFC is tonically up-regulated during performance of the communicative task, with planning and observation of actions evoking opposite computational loads in this region with respect to the pre- and postepoch phases. A third temporal profile of γ-band activity was found in the right posterior superior temporal sulcus (pSTS), a region previously reported to increase its metabolic demands as a function of communicative difficulty, both for Communicators generating novel communicative actions and Addressees trying to decode those signals (41). Differently from the ventral portions of the right TL and the vmPFC, the right pSTS is sensitive to computational demands that occur early in planning and that rise during action observation (pSTS; Fig. 3).

**Communicative Consequences of Tonic Up-Regulation of γ-Band Power.** The γ-band power changes described above were spatially and functionally specific, as illustrated by the absence of a tonic up-regulation of γ-band power during the same task epochs in a primary sensory area [right calcarine fissure (CF); Fig. 3, bottom row], despite strong transient changes in γ-band power time-locked to the presentation of the visual stimuli. A fourth analysis tested whether those tonic γ-band power changes are behaviorally relevant, with measurable consequences on the performance of the communicative task. We assessed trial-by-trial correlations of neural activity and behavioral performance (*SI Materials and Methods*). γ-Band activity measured during the baseline period preceding the occurrence of observable events predicted the planning time of the subsequent trial epoch both when solving communicative and instrumental problems (both as Communicator/Salesman, or as Addressee/Roadworker). Critically, the spatial distribution and magnitude of the baseline neural activity predicting task performance differed as a function of the current cognitive set. During the communicative task, tonic baseline activity in the right TL [of both Communicator (epoch C) and Addressee (epoch D); Fig. 1] predicted planning time in the same trial [Communicator: epoch D; Addressee: epoch F; $r = 0.07 \pm 0.02$; $t(23) = 2.5$; $P < 0.03$; Fig. 4 *A* and *C*]. The spatial distribution of this effect overlaps with the changes in γ-band activity shared across the two communicators (Fig. 2*E*). In contrast, during the instrumental task, tonic baseline activity in the parietooccipital cortex (of both Salesman and Roadworker) predicted planning time in the same trial [$r = 0.09 \pm 0.02$; $t(23) = 3.5$; $P < 0.05$; Fig. 4 *B* and *C*]. The spatial distribution of this effect overlaps with the known contribution of the parietooccipital cortex in supporting visuospatial transformations during action planning (42) and with the observation that planning time during the instrumental task was linearly related to the number of movement steps performed by the subjects in the subsequent task epoch. In both tasks, there were no significant correlations between tonic baseline activity and planning time in the preceding trial ($r = 0.02 \pm 0.02$ for each task).

## Discussion

This study describes the spectral, spatial, and temporal features of neural activity evoked during the selection and comprehension of novel shared symbols, two processes essential for understanding the flexibility of human communication (3, 5). There are three main findings. First, solving novel communicative problems up-regulated local neural activity in the right ventrolateral TL and the vmPFC, two regions necessary for processing conceptual knowledge and mental models of other agents (23, 43, 44). Second, the same up-regulation of neural activity was found across Communicator and Addressee, irrespectively of whether a communicative action was being selected or comprehended. This finding indicates that the overlapping neural up-regulation was driven by abstract task features shared across interlocutors, rather than sensorimotor events which differed between interlocutors. Third, the overlapping neural up-regulation was present well before the occurrence of a specific communicative problem. This finding provides a neural counterpart to the notion that the meaning of novel communicative actions is inferred by embedding those stimuli in a conceptual space whose activation predates in time the processing of the communicative stimuli themselves (45). Taken together, these observations indicate that the brain solves the computational challenges evoked by creating novel shared symbols by up-regulating the same neuronal mechanism in the same brain regions across pairs of communicators, and over temporal scales independent from transient sensorimotor events (46).

**Tonically Increased Neural Activity During Communicative Interactions.** The up-regulation of neural activity evoked by the presence of communicative demands had specific spatial, spectral, and temporal characteristics. First, the spatial distribution of differential neural activity between the communicative and the instrumental task was confined to the right temporal and medial prefrontal regions. These two areas have been shown to be necessary for accessing conceptual knowledge and mental models of other agents (23, 43, 44). Second, the spectral profile of this differential source-reconstructed neural activity was extremely broad. Physiologically, broadband shifts of local neural activity are functionally distinct from band-limited neuronal oscillations (47), and they are thought to reflect changes in mean firing rates of neuronal populations (48–51). Population-level firing rates have been shown to be affected by internal cortical states as much as by external stimuli (52, 53), and they are instrumental for integrating driving afferences with contextual information (54–56). Third, the temporal profile of the broadband shift of neural activity started already during the baseline epoch, before the presentation of a particular communicative problem and well before the observation of communicative actions. This baseline-related local

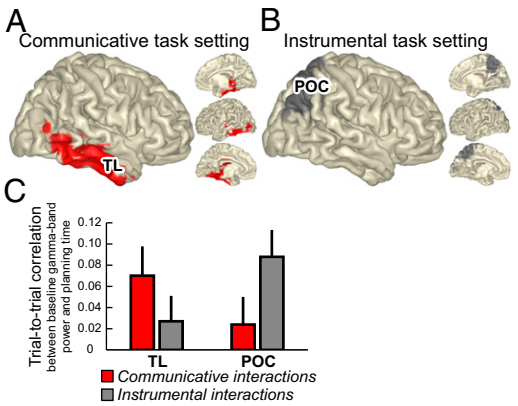


**Fig. 4.** Ongoing neural activity associated with the cognitive set. (*A* and *B*) Spatial distribution of cortical regions showing trial-by-trial correlation between baseline neural activity and task performance. Baseline γ-band (55–85 Hz) power in the TL accounted for variation in planning time of Communicators and Addressees; baseline γ-band power in the parietooccipital cortex (POC) accounted for variation in planning time of Salesmen and Roadworkers. (*C*) Group-averaged correlations for each of the two tasks and cortical regions (±1 SEM).

neural activity had measurable behavioral consequences on communicative performance during a subsequent epoch in the same trial (Fig. 4), and it fits with the behavioral observation that these subjects displayed audience design during trials following a communicative error (36). Taken together, these observations suggest that the tonic up-regulation of broadband neural activity evoked by communicative challenges reflects increased firing rates of neuronal populations in the right ventrolateral TL and the vmPFC. Those increased firing rates might provide a neurophysiological mechanism for integrating the current communicative problem with conceptual knowledge. Crucially, the present data suggest that this integration is not temporally bound to the presentation of a specific communicative problem in the course of a trial. In fact, the current findings support the notion that conceptual knowledge during a communicative interaction needs to be continuously aligned to the conversational context and to the interlocutor's behavior (19). The tonic up-regulation of broadband activity observed in this study during communicative interactions might be a neural marker of this cognitive phenomenon.

**Shared Tonic Computations Between Production and Comprehension of Communicative Actions.** A large portion of the right TL showed a sustained increase in broadband activity during both planning and understanding of communicative actions. This finding qualifies the characteristics of the coarse spatiotemporal cerebral overlaps between communicators reported in previous studies (30, 33, 41, 57). Namely, the presence of a spectral overlap between communicators suggests that the human brain uses the same neurophysiological mechanisms when planning and understanding communicative actions. Given that those two epochs had considerable sensorimotor differences, and that the spectral overlap arose from brain regions necessary for processing conceptual knowledge and mental models of other agents, it is conceivable that Communicators and Addressees might share a basic conceptual mechanism that supports a rapid exploration through a large search space (41).

**Shared Phasic Computations During Social and Nonsocial Behaviors.** This study shows that solving complex communicative and instrumental problems relies on computational processes with surprisingly matched phasic neural dynamics. For instance, γ-band power in the vmPFC transiently increased during the selection of complex action sequences, irrespectively of the communicative characteristics of those actions. The within-trial fluctuations of γ-band power in pSTS also showed a strikingly similar pattern when solving communicative compared with instrumental problems. These findings suggests that vmPFC and pSTS are involved in selecting communicative actions using neural dynamics similar to those involved in selecting noncommunicative actions (8). This observation argues against the notion that these two regions are exclusively dedicated to social cognition (12).

## Conclusions

Humans are surprisingly effective at creating novel shared symbols (6, 18), an evolutionary anomaly at the root of human communication (3, 5). This study describes the spectral, temporal, and spatial characteristics of neural activity evoked during planning and understanding of novel communicative actions. The computational challenges evoked by solving communicative problems result in tonically up-regulated neural activity over right temporal and ventromedial prefrontal regions. The phasic temporal dynamics of those regions was sensitive to the occurrence of transient sensory or motor events, but it was indifferent to the communicative characteristics of the problems. These findings define the neurophysiological characteristics of a mechanism supporting human communicative innovation, opening the way for understanding the neural implementation of human symbolic communication.

## Materials and Methods

**Participants.** Fifty-two participants (22 males and 30 females; ages, 18–40 y), were recruited to take part in this study. They were screened for a history of psychiatric and neurological problems and had normal or corrected-to-normal vision. Participants gave informed consent according to institutional guidelines of the local ethics committee (Committee on Research Involving Human Subjects, region Arnhem-Nijmegen, The Netherlands; approved by Radboud University Nijmegen) and were either offered a financial payment or given credits toward completing a course requirement. Magnetoencephalographic activity was acquired from one member of each pair. Two pairs of participants were excluded from data analysis because of MEG-system failure and muscle artifacts, leaving 24 pairs of participants for data analysis.

**Tasks.** The communicative and the instrumental tasks are described in detail in *SI Materials and Methods*.

**MEG and MRI Data Acquisition.** Brain activity was recorded over two sessions using a whole-head MEG with 275 axial gradiometers (CTF275; VSM MedTech; 1,200-Hz sampling rate; 300-Hz analog low-pass filter). Before the second session, each participant repositioned his or her head in the same location and orientation as the position measured before the first session, using a real-time head localizer tool (58). Anatomical images of the brain for forward model generation (voxel size, 1 $mm^3$) were acquired using a 1.5T Siemens Avanto scanner. During MR acquisition, identical earplugs (with a vitamin E capsule in place of the MEG localization coils) were used for coregistration of the MRI and MEG data.

**MEG Data Analysis.** Data were analyzed offline using the FieldTrip toolbox (59) and custom MATLAB code (MathWorks). Trials with muscle and MEG artifacts were removed from the MEG time series, resulting in 91 ± 5% of the original trials being included for further analysis. Following our experimental rationale, we focused the analysis of the MEG data on the trial epochs during which the Communicator and Salesman planned their actions (epoch D: planning; Fig. 1), and the Addressee and Roadworker observed the other player's movements (epoch E: observation). For each epoch, we also considered the preceding baseline period (1 s), during which only the empty grid was visible. We analyzed these task epochs in two ways, differing in the time scale at which the inferences can be drawn.

In analysis 1, we considered the whole time interval covered by the planning and observation events. Accordingly, we extracted the overall changes in cerebral neural activity evoked during those events, using adaptive spatial filtering (beamforming; *SI Materials and Methods*) to estimate local neural population activity throughout the brain as a function of frequency. We matched the signal-to-noise ratios of the different conditions within each participant by ensuring that each condition contributed the same number of samples to the data analysis. To achieve this, each trial was segmented into multiple consecutive nonoverlapping windows of 500 ms.

For each participant, windows were randomly selected and excluded from subsequent analyses until the different conditions provided the same number of windows. Then, the windowed time series from each trial epoch were tapered with a set of 4 orthogonal Slepian tapers before spectral estimation and the resulting estimates of the (cross-)spectral densities were averaged across tapers. This resulted in a spectral smoothing of ±5 Hz.

In analysis 2, we extracted the fine-grained temporal dynamics of power changes during the task epochs mentioned above, performing a time-frequency analysis at the source level. This analysis was time-locked to the moments the Communicator and Salesman started and finished planning (epochs D: planning) and the Addressee and Roadworker started and finished observing (epochs E: observation), extending over a time window of 2.75 s (range: −0.5 to +2.25 s and −2.25 to +0.5 s, respectively; resolution: 50 ms). We applied an adaptive spatial filtering approach within a set of frequencies (55–85 Hz) shown to contain task-relevant neural activity by analysis 1. Here, 200-ms windows were tapered with three orthogonal Slepian tapers (±10-Hz smoothing) before applying the Fourier transforms. Projection of the sensor-level data through the spatial filters, and subsequently computing the magnitude squared, yielded a location-specific (absolute) estimate of the time course of spectral power at the frequency of interest.

**Statistical Model and Inference.** We considered differential effects evoked during corresponding trial epochs in participants playing the Communicator or the Salesman role (epoch D: planning in Fig. 1) and the Addressee or the Roadworker role (epoch E: observation). First, we estimated participant-specific effects (independent samples *t* tests) on signal power at the source level (obtained from analysis 1) for each of these two sets of temporally independent comparisons. Second, these participant-specific effects were *z*-normalized to account for differences in degrees of freedom and entered into a second-level random effects analysis correcting for multiple comparisons at the cluster level ($P < 0.05$; 10,000 randomizations) (60). Third, the resulting group statistics of the two contrasts were entered into a conjunction analysis (34), effectively implementing a logical AND relation between the individual contrasts.

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# Supporting Information

## Stolk et al. 10.1073/pnas.1303170110

### SI Materials and Methods

**Experimental Setting.** Each pair of participants engaged in two types of real-time sequential interactive tasks, a communicative task and an instrumental task (Fig. 1), with the order of presentation of the two tasks counterbalanced over participant pairs. The interactions between participants took place on a digital grid, visually presented and computer-controlled. Each participant controlled the movements of a token on the game board by means of a hand-held controller. Four buttons controlled by the right thumb moved the token to the left, right, up, and down, respectively; the right shoulder button rotated the token 90° clockwise; and the left shoulder button was used as a start and end button. During the experiment, one participant was supine on a bed inside a magnetically shielded and sound-proof room. This participant was facing a projection screen and holding a magnetoencephalography (MEG)-compatible hand-held controller. The visually presented digital game board subtended a visual angle of ∼2° to minimize eye movements. The other participant sat outside the magnetically shielded room, in front of a 19-inch liquid-crystal-display monitor, using a structurally identical hand-held controller and wearing a sound-proof headset.

**Experiment Details.** An experiment lasted about 3 h with the following sequence of experimental sessions: preparation of the participants [delivery of instructions and placement of electrodes for electrocardiogram (ECG) and electrooculogram (EOG); ∼20 min]; training with using the hand-held controller (∼15 min); training in the first interactive game (20 trials; ∼20 min); performance/recording of the first interactive game (80 trials; ∼45 min); training in the second interactive game (20 trials; ∼20 min); performance/recording of the second interactive game (80 trials; ∼45 min); and acquisition of an MR anatomical scan (∼15 min). Task events within each training and performance sessions were programmed using Presentation 9 (Neurobehavioral Systems) and run on a Windows XP personal computer handling visual presentation, receiving triggers from the hand-held controllers, and marking task events through triggers sent to the MEG-acquisition system.

**Communicative Interaction.** This task involves two players alternating between the roles of Communicator and Addressee across successive trials. At trial onset, each player is assigned a role and a token (Fig. 1, *Left*, epochs A and B: role and token assignment). After a baseline epoch consisting of an empty grid display (epoch C: baseline period), the Communicator (and the Communicator only) is shown the target configuration of that trial (epoch D: planning). The target configuration contains the tokens of the Communicator and the Addressee at the grid locations and orientations that they should have at the end of the trial. The Communicator knows that the Addressee does not see the target configuration and that he cannot move the Addressee's token. Therefore, the Communicator needs to communicate to the Addressee the location and orientation that her token should have at the end of the trial. To comply with the task requirements, the Communicator also needs to ensure that at the end of his turn his token is at the location and orientation specified by the target configuration. In this game, the only means available to the Communicator for communicating with the Addressee is by moving his own token around the grid, namely horizontal translations, vertical translations, or clockwise rotations. Both Communicator and Addressee also know that the Communicator has unlimited time available for planning his moves but only 5 s for moving his token on the grid. The Communicator signals his readiness to move by pressing the start/stop button. At this point, the target configuration disappears, the Communicator's token appears in the center of the grid, and he can start moving his token (epoch E: movement). After 5 s, or earlier if the Communicator hits the start/stop button again, the Communicator's token cannot move further and the Addressee's token appears in the center of the grid. This event indicates that the Addressee has acquired control over her token. The Addressee has unlimited time to infer the target location and orientation of her token on the basis of the observed movements of the Communicator (epoch F: planning). After the Addressee presses the start/stop button, she has 5 s to move her token (epoch G: movement). Finally, after 5 s, or earlier if the Addressee hits the start/stop button again, the same feedback is presented to both players in the form of a green tick or red cross (positive or negative feedback, respectively; epoch H: feedback). The feedback indicates whether the participants had matched the location and orientation of their tokens with those of the target configuration.

Two important features of this communicative task should be emphasized. First, the Addressee cannot solve the communicative task by reproducing the movements of the communicator's token. Rather, the Addressee needs to disambiguate communicative and instrumental components of the communicator's movements and find some relationship between the communicator's movements and their meaning. Second, there are no a priori correct solutions to the communicative task, nor is there a limited set of options from which the Communicator could choose.

**Instrumental Interaction.** In this task, two players alternated between the roles of Salesman and Roadworker across successive trials. At trial onset, each player is assigned a role and a token (Fig. 1, *Right*, epochs A and B: role and token assignment). After a baseline epoch consisting of an empty grid display (epoch C: baseline period), only the Salesman is shown the target configuration of that trial (epoch D: planning). The target configuration contains the tokens of the Salesman and the Roadworker. Differently from the communicative task, the target configuration of the instrumental task defines the trial-specific conditions of a problem that the Salesman needs to solve individually. Namely, the goal of the Salesman is to select a path of translations of his token through the grid, passing through a set of waypoints, in the following sequence: point 1, starting position in the center of the grid (where the Salesman's token is placed at the end of the planning phase); point 2, location of the Salesman's token as displayed in the target configuration (labeled as Salesman's "home" for clarity); point 3, location and orientation of the token displayed in the target configuration that is different from the Salesman's token (labeled as the "outlet" for clarity); and point 4, location of the Salesman's home. The Salesman needs to satisfy a further requirement, namely he needs to pass exactly twice through one grid location different from the Salesman's home (that is also meant to be visited twice, see points 2 and 4 above). As in the communicative task, during the instrumental task, the Salesman has unlimited time available for planning his moves but only 5 s for moving his token on the grid. The Salesman signals his readiness to move by pressing the start button. At this point, the target configuration disappears, the Salesman's token appears in the center of the grid, and he can start moving his token (epoch E: movement). After 5 s, or earlier if the Salesman hits the start button again, the Salesman's token cannot move further and the Roadworker's token appears in the center of the grid. This event indicates that the

Roadworker has acquired control over her token. Similarly to what happened for the Addressee in the communicative task, the task of the Roadworker in the instrumental task depends on the movements of the coplayer (i.e., Salesman). However, differently from the communicative task, in the instrumental task, the Roadworker uses inadvertently displayed features of the Salesman's movements to solve her task. Namely, the Roadworker is asked to move to the grid location visited twice by the Salesman, excluding the Salesman's house. The Roadworker has unlimited time to decide where to move her token on the basis of the observed movements of the Salesman (epoch F: planning). After the Roadworker presses the start button, she has 5 s to move her token (epoch G: movement). Finally, after 5 s, or earlier if the Roadworker hits the start button again, feedback is presented to the two players in the form of a green tick or red cross (positive or negative feedback, respectively; epoch H: feedback). The feedback indicates to each player independently whether they had complied with the requirements of the instrumental task on that trial.

**Manipulations of Task Difficulty.** In both the communicative and instrumental task, we increased task difficulty across successive trials (for examples, see Fig. S1 *A* and *B*). In the communicative task, the rationale of this intervention was to drive participants to continuously create new communicative behaviors, rather than exploiting already-established communicative conventions. Communicative-task difficulty was increased by introducing deliberate mismatches between the geometrical characteristics of the tokens of Communicators and Addressees. For instance, when the Communicator's token was a circle and the Addressee's token was a triangle (Fig. S1*A*, middle column), then the Communicator needed to find a new way to indicate to the Addressee the orientation of her token, because rotations of the circle token were not visible. A further level of difficulty could be introduced by using a triangular token pointing outward the grid as the Addressee's target configuration, the Communicator's token being a circle (Fig S1*A*, right column).

In the instrumental task, the rationale was to match the surface behavior evoked in the communicative task. Instrumental-task difficulty was also increased by introducing triangular shaped tokens for the Roadworker (the outlet). Outlets with a triangular token required the Salesman to leave the outlet along the direction to which the token was pointing and to enter it from any but the same side ("one-way rule"; Fig. S1*B*, middle column). A further level of difficulty could be introduced by using a triangular token as the Salesman's home because, then, the same rule would also apply to that location (Fig. S1*B*, right column). Triangular tokens would also increase task difficulty for the Roadworker. Namely, if the Roadworker's token was a triangle, her task would then involve rotating her token such that the triangle pointed to the direction of the movement of the Salesman's token when it left that revisited location the second time.

**Behavioral Data Analysis.** We considered mean planning times, mean movement times, and mean number of moves of Communicator and Addressee in the communicative task and Salesman and Roadworker in the instrumental task (Fig. S1). These dependent variables were calculated for each of the 24 pairs of participants and for each of the two tasks and compared statistically by means of paired $t$ tests (two-tailed $\alpha$-level: 0.05). We also compared the mean time spent on target locations and on nontarget locations (within-movement epochs E; Fig. 1) separately for each game, in a two-way ANOVA with task setting (communicative, instrumental) and location (target, nontarget) as factors. In the communicative task, the target refers to the Addressee's target location that had to be communicated by the Communicator. In the instrumental task, the target was defined as the location that had to be visited twice by the Salesman and reached by the Roadworker. Nontarget locations were defined as the other grid locations visited by the Communicator or by the Salesman. We considered pairs of participants as the unit of observation for the statistical analysis because in the communicative task, performance is dependent on both elements of a pair, and, for consistency, we adopted the same approach with the instrumental task. Finally, we considered the percentage of correct trials achieved by the participants in the communicative and instrumental task. Given the task characteristics, correct outcome could be defined on the basis of individual performance in the instrumental task but only on the basis of joint performance in the communicative task. Accordingly, we refrained from directly comparing performance between the two tasks.

**MEG Source Reconstruction.** Participant-specific anatomical MRIs were used to linearly transform a 3D template grid (10-mm spacing) in Montreal Neurological Institute coordinates to the coordinate system specific to the participant's head. To this end, we used SPM8 (Statistical Parametric Mapping; www.fil.ion.ucl.ac.uk/spm) to estimate the affine transformation between the two coordinate systems. We subsequently applied the inverse of this transformation to obtain grid positions at matched brain locations across participants. For each of the positions on that grid, neural activity was estimated using a frequency-domain "beamforming" approach. This method constructs spatial filters for each of the grid positions, passing the activity from the location of interest with unit gain, while maximally suppressing activity from all other possible sources of neural and nonneural electrical activity. The beamformer spatial filter is constructed from the lead field and the cross-spectral-density matrix of the data. The lead field is the physical forward model of the field distribution calculated from an assumed source at a given location and the participant-specific volume-conduction model of the head. Here, we used a single-shell volume-conduction model of the brain, based on the brain boundary determined by the segmented anatomical MRI and computed the lead fields according to ref. 1. In this study, we considered spatial filters generated by using condition- and participant-specific lead fields. This approach takes into account and controls for differences in head position and orientation of the sources relative to the MEG sensors, leading to more consistent and less biased estimates of source-level effects across participants and conditions.

**General Assessments of Neurophysiologic Data.** The participant's head position relative to the MEG sensors was measured before, during, and after each session using localization coils, placed at the nasion and the left and right ear canals. Before the second session, each participant was asked to reposition his/her head in the same location and orientation as the position measured before the first session, using a real-time head localizer tool (2). To test for systematic differences in head positions, we computed the difference in the position of the center of the head between the two sessions for all participants. The average position difference along the axis accounting for most of the variance was $0.6 \pm 0.4$ mm (mean $\pm$ SEM), an indication of strong intersession consistency in head location.

Electrocardiogram (ECG) traces and vertical and horizontal electrooculogram ($EOG_v$ and $EOG_h$) traces were recorded during task performances, using three pairs of 10-mm diameter Ag-AgCl surface electrodes with bipolar montages. The ECG showed no statistically significant differences in heart rate [communicative setting $69.2 \pm 1.8$ bpm versus instrumental setting $69.5 \pm 2.1$ bpm (mean $\pm$ SEM)]. The EOG traces showed no statistically significant differences in overall signal energy: Communicator vs. Salesman, $t(23) < 0.8$; and Addressee vs. Roadworker, $t(23) > -1.4$ (paired samples $t$ tests).

To provide a more stringent filter against the effects of eye movements on the spatial distribution of task-related effects and on the temporal dynamics of source-reconstructed activity, we directly

removed continuous eye movement estimates from the source-reconstructed MEG data before further analyses. The contribution of vertical ($EOG_v$) and horizontal ($EOG_h$) electrooculographic signals was estimated in the same time segments and frequency bands as that of the source-reconstructed signal and removed from that signal, according to the following procedure:

$$\mathbf{Y} = \mathbf{b}_0\mathbf{C} + \mathbf{b}_1\mathbf{EOG}_v + \mathbf{b}_2\mathbf{EOG}_h + \mathbf{E},$$

where Y is source data over K trials, $b_0$ is the intercept constant, C is a K vector of ones, and $b_1$ and $b_2$ are regression coefficients for eye movement-related activity recorded at the vertical and horizontal EOG channels, respectively. E is unexplained model error. The least-squares solution to the linear equation,

$$min||\mathbf{Y} - \mathbf{b}_0\mathbf{C} - \mathbf{b}_1\mathbf{EOG_v} - \mathbf{b}_2\mathbf{EOG_h}||^2,$$

then results in three b values per voxel (two for the EOG channels and one constant). Subsequently, the estimated contributions of the EOG regressors to the source reconstructed spectral power were removed from the original single-trial source data:

$$\mathbf{Y}_{clean} = \mathbf{Y} - \mathbf{b}_1\mathbf{EOG_v} - \mathbf{b}_2\mathbf{EOG_h},$$

where $Y_{clean}$ represents the data with eye movement-related variance removed (and with the intercept constant remaining in the data). Fig. S3 illustrates the spatial distribution of beta values estimated for each EOG channel (vertical and horizontal) and epoch type (planning and observation of actions). It can be seen that the EOG signal in the 55- to 85-Hz band was significantly correlated with source-reconstructed activity from orbitofrontal cortex, most likely because of both locations picking up activity of the extraocular muscles involved during saccades (3, 4).

**Trial-by-Trial Coupling Between Baseline Neural Activity and Task Performance.** The source level trial-by-trial γ-band powers were ensured free from head movements (2) before computing trial-by-trial correlations between γ-band activity and planning times in a subsequent trial epoch. The planning times (i.e., Communicator/Salesman and Addressee/Roadworker in trial epochs D and F, respectively) were log-transformed, and both dependent variables were normalized per task role separately before concatenation (with equal number of trials per interaction type) and subsequent correlation. The significance of the coupling was tested by testing the *z*-transformed single-subject correlations against null at the group level.


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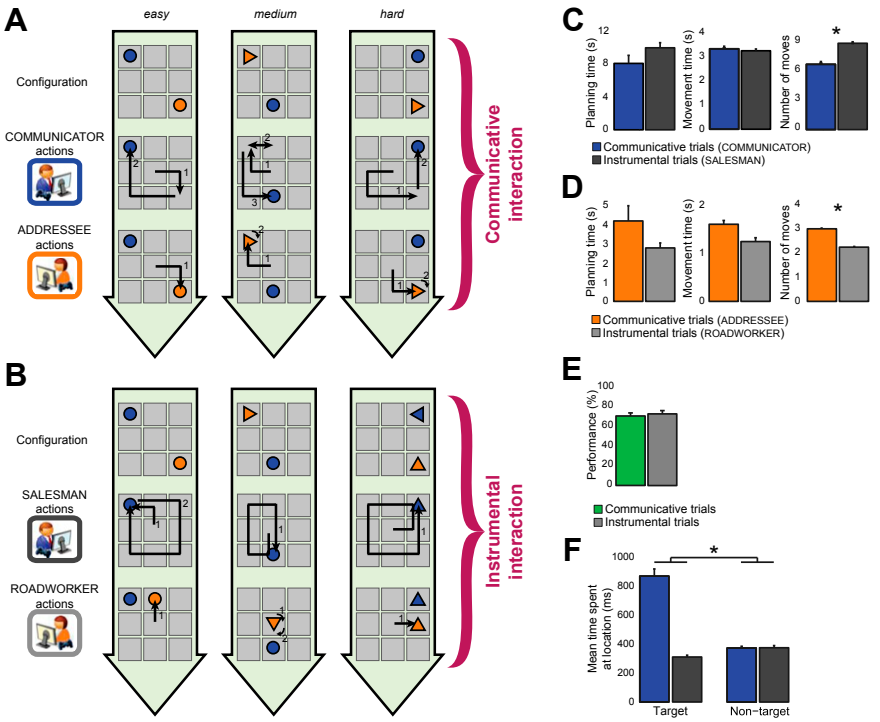



**Fig. S1.** Representative examples (*A* and *B*) and summary statistics (*C–F*) of interactive behaviors in the communicative and instrumental tasks. (*A* and *B*) Each column shows representative examples of interactive behaviors at three different levels of task difficulty, separately for communicative interactions (*A*) and instrumental interactions (*B*). The first row describes the initial problem faced by the Communicator (*A*) and by the Salesman (*B*). This task epoch corresponds to epoch D in Fig. 1. The second row in *A* and *B* describes the actions of the Communicator/Salesman (see epoch E in Fig. 1) [i.e., horizontal/vertical translations (arrows), sequences of translations (broken arrows), return translations (double arrows), and 90° clockwise rotations (small curved arrows)]. The third row in *A* and *B* describes the actions of the Addressee/Roadworker (see epoch H in Fig. 1). Below, we provide an account of some frequently observed interactive behaviors. "Communicative interaction—Easy": the Communicator moves toward the Addressee's target grid location (orange token), pauses, and then moves his token to the Communicator's own target location (blue token). The pause is dysfunctional to the Communicator's goal of reaching his target. The Addressee infers that this instrumentally dysfunctional behavior performs a communicative function, marking the location that her token should have on the grid. "Communicative interaction—Medium": the Communicator moves toward the Addressee's target grid location, pauses, and then moves one grid location along the direction the triangle is pointing to, moves back to the Addressee's target location, pauses again, and then moves to the Communicator's own target location. The "wiggling" signal (i.e., moving one grid location aside and back, depicted by the double arrow) is a more complex instrumentally dysfunctional behavior that assumes a communicative value, providing the Addressee with an indication for the orientation that her token should have on the grid. "Communicative interaction—Hard": the Communicator makes a detour before going toward the Addressee's target location, pauses at the Addressee's target location, and then goes to the Communicator's own target location. Marking the orientation of a token pointing outward on the grid cannot be mapped to the communicative behaviors described above. Communicators solve this problem by exploiting the conversational context set by the previous examples, namely avoiding to produce "wiggles," and marking this absence with an instrumentally dysfunctional detour. The absence of an orientation signal (the wiggles), together with an ostensive cue marking the salience of that absence (the detour), provides a new communicative signal that is interpreted as indicating a token orientation that cannot be marked by the "wiggle strategy." Please note that this is only one among a series of possible solutions. For instance, some Communicators use the number of subsequent wiggles to mark the number of clockwise rotations that the Addressee needs to make to achieve the target orientation of her token. "Instrumental interaction—Easy": the Salesman moves toward the Salesman's home (blue token) and returns to the grid location from which he came and has now visited twice. He then moves toward the outlet (orange token) and subsequently to his home again, while avoiding revisiting another grid location. There are three alternative solutions, of which two include the revisiting of the center left grid location instead. The Roadworker moves toward the grid location visited twice by the Salesman to achieve her objective ("repairing" the grid location visited twice by the Salesman). "Instrumental interaction—Medium": the Salesman visits the home location, then the outlet while obeying the one-way rule associated with the triangle's orientation (a triangular token required the Salesman to leave that grid location along the direction to which the token was pointing and to enter it from any but the same side), and subsequently moves toward the home while revisiting the center field (the start at the center grid counts as one visit to this location). The Roadworker stays at the center grid but rotates her token such that the triangle points to the direction of movement of the Salesman's token when it left that revisited location the second time, thus achieving her objective (*SI Materials and Methods*, *Manipulations of Task Difficulty*). "Instrumental interaction—Hard": although the Salesman now has to move along the one-way rules of two tokens, there is only one solution to his problem. The Salesman moves to the right, so he can enter and leave his home along the direction of the triangle's point, and then moves around the grid toward the outlet while not revisiting any other grid location. He subsequently enters and leaves the outlet along the direction that the triangle is pointing to and revisits a previously visited grid location for the first time before returning home. The Salesman does not need to match any orientation with his own token. The Roadworker's token is triangular-shaped and, therefore, needs to match the Salesman's movement direction (similar to the Medium example). However, because her token's orientation at start already matches the target orientation of this trial, she moves toward the Salesman's revisited location without making any additional rotations. (*C*) Planning times (epoch D in Fig. 1), Movement times (epoch E in Fig. 1), and Number of moves of Communicators and Salesmen. Note that the Communicator and Salesman Movement times determine the Addressee and Roadworker observing times. (*D*) Planning times (epoch F in Fig. 1), Movement times (epoch G in Fig. 1), and Number of moves of Addressees and Roadworkers. Note that Addressees make more moves than Roadworkers, whereas Communicators make fewer moves than Salesmen. Therefore, task-related differential effects common to Communicators and Addressees (Fig. 2*E*) cannot be driven by these behavioral differences in task performance. (*E*) Percentage of successful trials in the communicative and instrumental task. Note that, in the communicative task, successful performance is conditional on both players (green bar); the same parameter is provided for the instrumental task (gray bar). (*F*) Mean time spent at grid locations within the movement intervals, separately for target and nontarget locations (in each case the average per trial is taken). In the communicative trials, target refers to the Addressee's target grid location that had to be communicated by the Communicator. For the instrumental trials, target refers to the location that was meant to be visited twice by the Salesman. The nontarget locations refer to other visited locations on the digital grid. Error bars indicate ±1 SEM. $^*P < 0.001$.

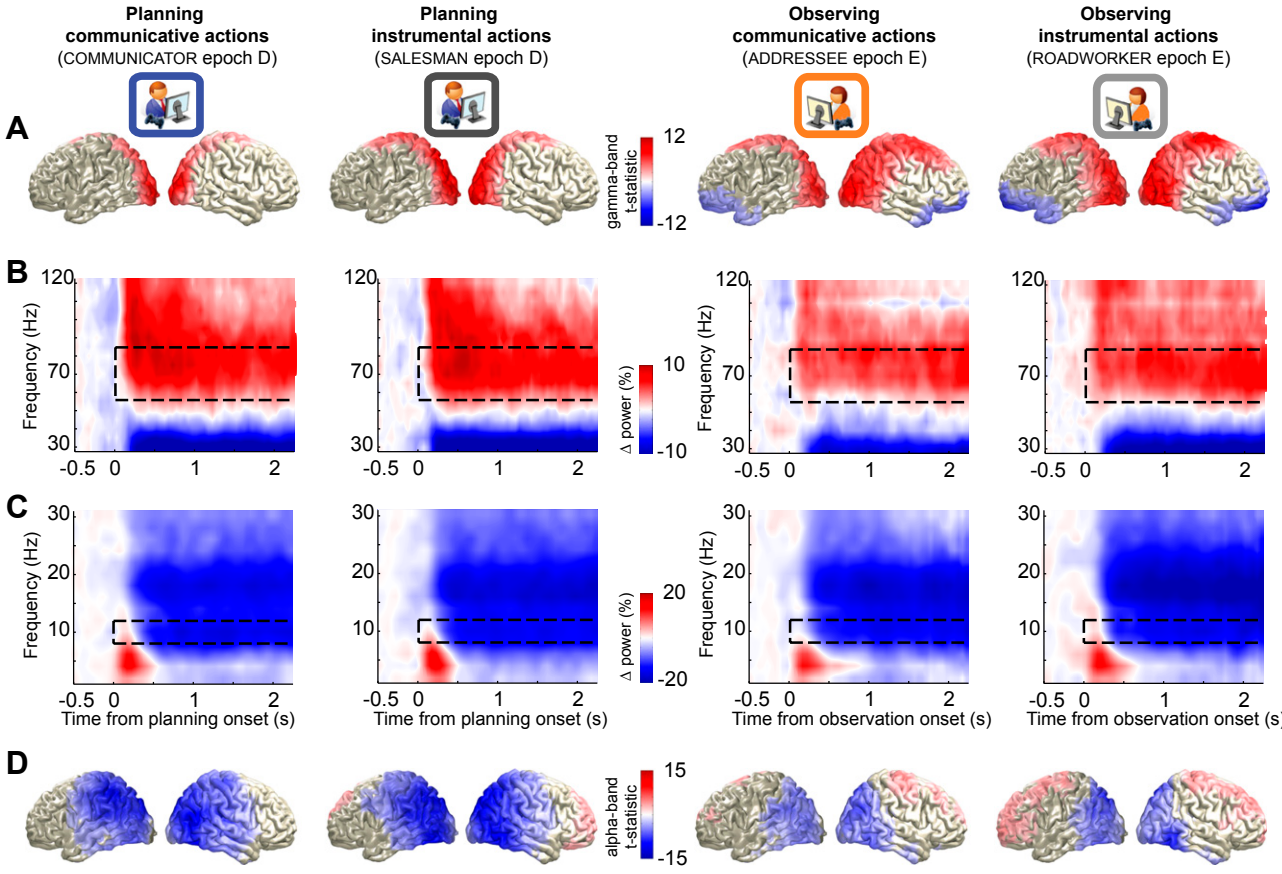



**Fig. S2.** Spatial, spectral, and temporal profile of task-related neural activity (*A*–*D*). The task-evoked modulations in signal power (relative to baseline) indicate highly comparable patterns of induced neural activity in the sensorimotor system (occipital and posterior parietal cortex) within the two planning epochs (Communicator and Salesman; first and second column) and within the two observation epochs (Addressee and Roadworker; third and fourth column). The top two rows (*A* and *B*) represent the spatial, temporal, and spectral characteristics of changes in high-frequency power (>30 Hz) evoked by the task. This analysis was based on 200-ms windows tapered with a set of three orthogonal Slepian tapers. The bottom two rows (*C* and *D*) represent similar characteristics of changes in low frequency power (<30 Hz) evoked by the task. This analysis was based on 500-ms windows and a single Hanning taper. (*A*) Lateral views on functional source reconstructions of γ (55–85 Hz) activity evoked during the whole of the planning and observation epochs contrasted with the endmost second of their preceding baseline periods. (*B*) The power responses resolved in time and frequency in voxels that survived the multiple comparison statistics as a positive cluster in *A* ($P < 0.05$). (*C*) The power responses resolved in time and frequency in voxels that survived the multiple comparison statistics as a negative cluster in *D* ($P < 0.05$). (*D*) Lateral views on functional source reconstructions of alpha (8–12 Hz) activity evoked during the whole of the planning and observation epochs contrasted with the endmost second of their preceding baseline periods.

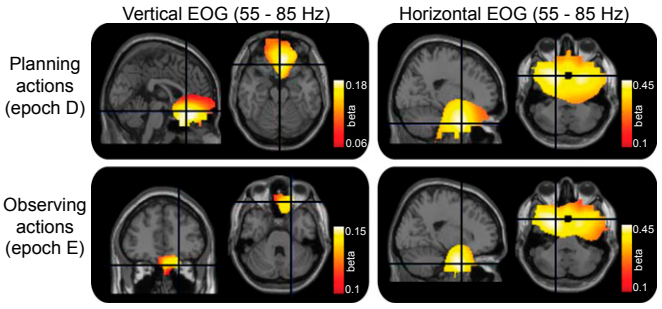



**Fig. S3.** Contributions from eye movement during the planning (top row) and observation of actions (bottom row) were estimated and regressed out from the source-reconstructed data before further analysis. The normalized beta-weights (obtained by normalizing the source and EOG data before multiple linear regression analysis) reveal the spatial structure of source-reconstructed activity (i.e., around the extraocular muscles, that is significantly correlated with vertical and horizontal EOG activity in the 55- to 85-Hz frequency range). The threshold of the color axis was raised to resolve the spatial structure around the statistically significant peaks (*t* value, >8; $P < 0.05$; multiple comparison-corrected). The upper β values are the peaks.

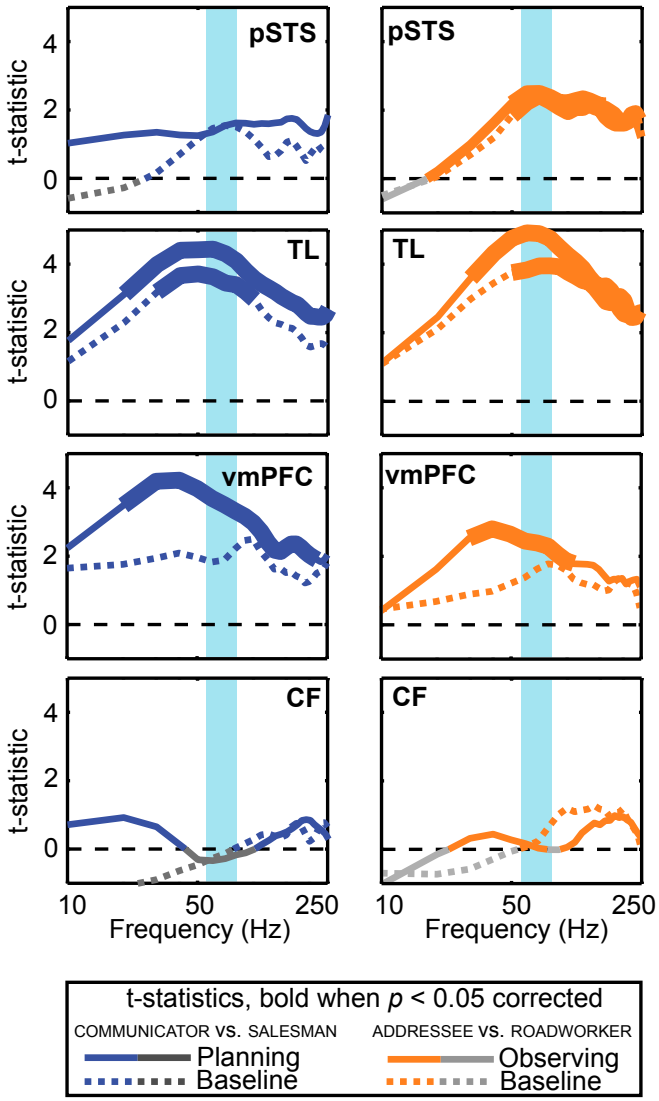
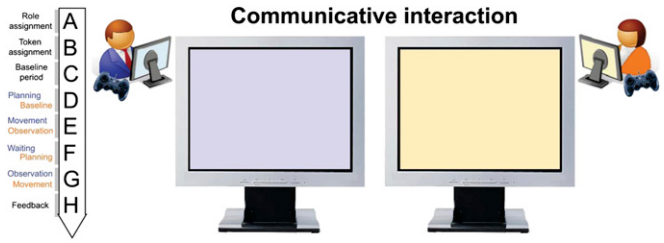
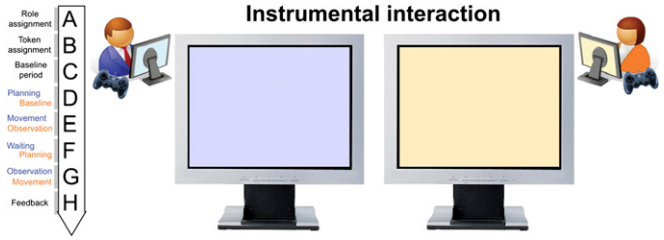



**Fig. S4.** The *t* statistics per frequency bin indicate that the differences in (absolute) neural activity between the communicative and instrumental task epochs were statistically most pronounced in the 55- to 85-Hz γ band (in cyan). The graphs follow the presentation order of the power spectral densities in Fig. 2 *B* and *D*. The solid lines represent the *t* statistics derived from group-level paired *t* tests on source-reconstructed cerebral neural activity evoked during the whole of the planning and observation epochs. The dashed lines represent the same contrasts but now regarding the endmost second of preceding baseline periods during which only the empty grid was presented.



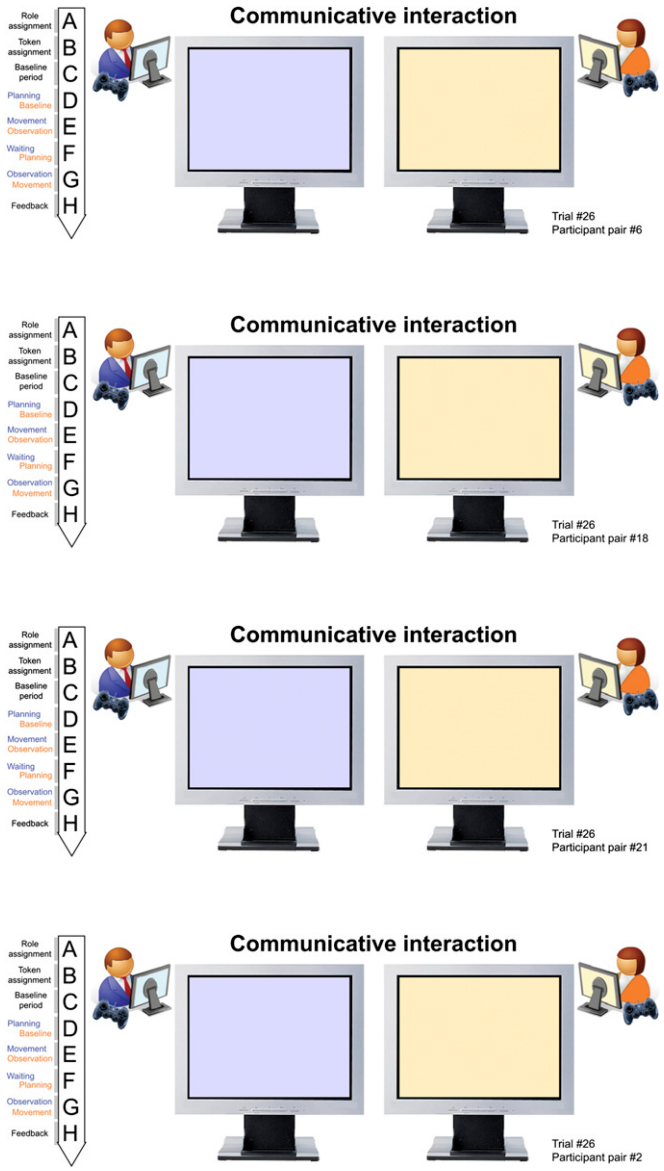

**Movie S1.** Representative example of interactive behavior in the communicative task. This movie illustrates the average timing of the participants during this task, with 1 s added before and after each transition across trial epochs to facilitate vision of the trial sequence. During a communicative interaction, a target configuration was shown to the Communicator only (Communicator epoch D). To achieve that target configuration, the Communicator needed to convince the Addressee to move her token (in orange) to the desired target location and orientation. The Communicator could achieve this only by moving his token (in blue) across the digital grid, knowing that the Addressee will observe those movements (Addressee epoch E) to decide where and how to move her token (Addressee epoch G). The success of a communicative interaction relied on the Communicator designing an action that could be understood by the Addressee (during planning in epoch D) and on the Addressee inferring the Communicator's intentions (during observation in epoch E).

Movie S1



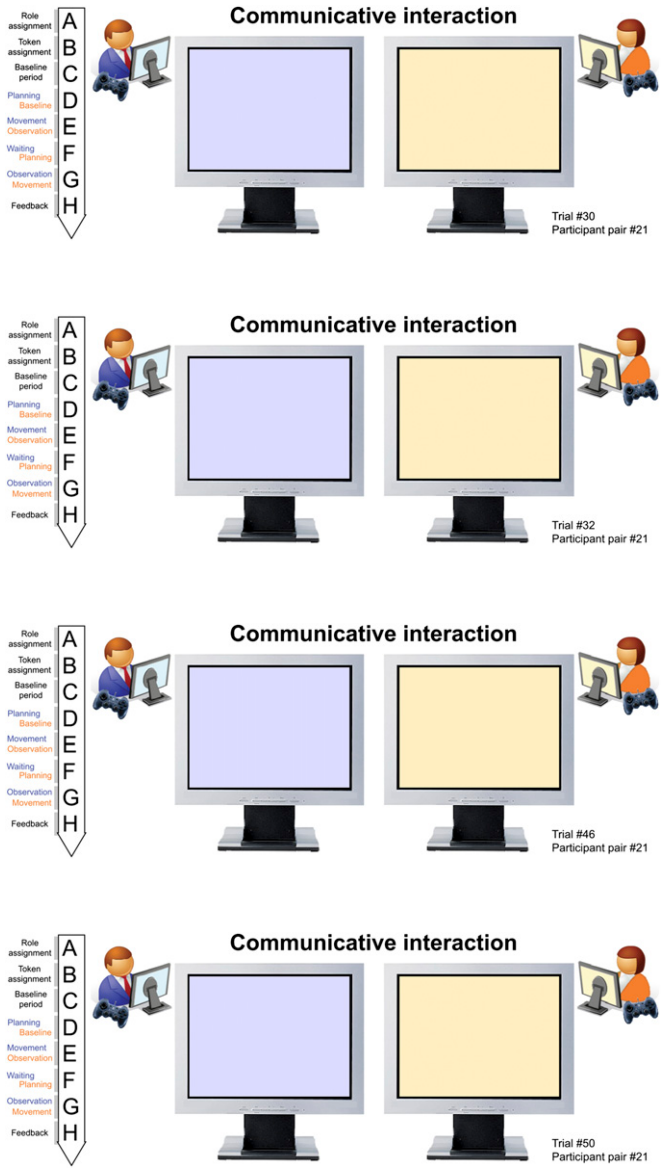

**Movie S2.** Representative example of interactive behavior in the instrumental task. This movie illustrates the average timing of the participants during this task, with 1 s added before and after each transition across trial epochs to facilitate vision of the trial sequence. During an instrumental interaction, the Salesman 's objective was to travel between two grid locations while visiting only one grid location twice (Salesman epoch D), knowing that the Roadworker will observe those movements (Roadworker epoch E) to decide where and how to move to the grid location visited twice (Roadworker epoch G). A triangular token required the Salesman to leave that grid location along the direction to which the token was pointing and to enter it from any but the same side (one-way rule). Concomitantly, it required the Roadworker to rotate her token such that the triangle pointed to the direction of the movement of the Salesman's token when it left the revisited location the second time. The success of an instrumental interaction relied on the Salesman designing an action according to pre-established rules (during planning in epoch D) and on the Roadworker implementing her assigned rules according to the behavior of the Salesman (during observation in epoch E).

Movie S2



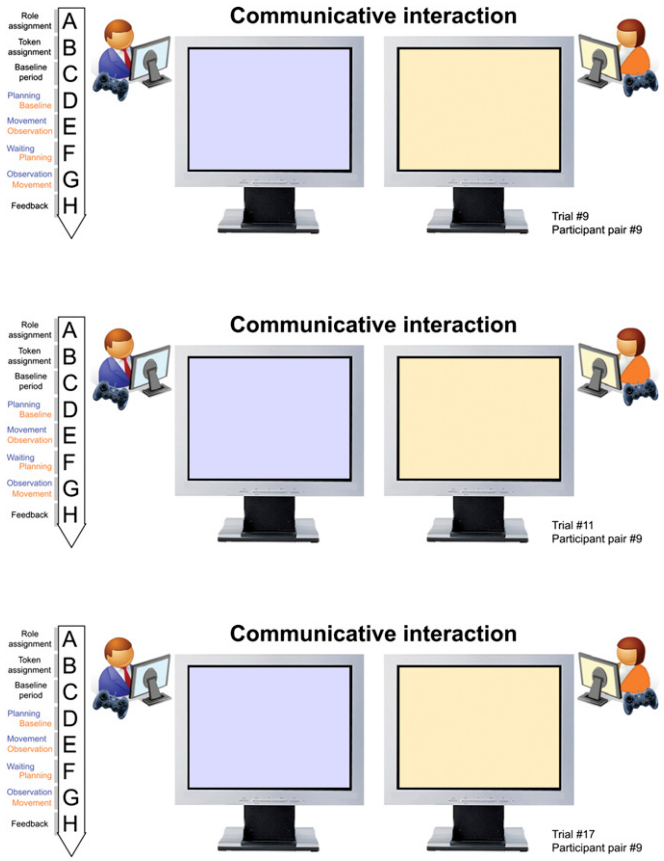

**Movie S3.** This movie and Movie S4 and S5 reproduce exactly the behavior of the participants recorded during the trials on display, with 1 s added before and after each transition across trial epochs to facilitate vision of the trial sequence. Interactive behaviors evoked during trial 26 of the communicative task in four different participant pairs. Three successful pairs showed different communicative behaviors, illustrating how different conversational contexts may evoke different communicative behaviors with the same meaning. For instance, subjectively interpreted, the Communicator of pair 6 briefly pauses on the target location and then uses an "exit-point strategy" to indicate orientation, leaving that grid location along the direction to which the triangular token needs to point (*A*). Communicator 18 uses an "entry- and exit-point strategy," making two additional rotations at the target location to emphasize the need for the Addressee to rotate (*B*). Communicator 21 moves to the target location and rotates as many times as the Addressee has to rotate (*C*). The interpretation of those behaviors is by no means trivial. For instance, in participant pair 2 (*D*), the Communicator makes a similar communicative behavior (two rotations at the target location) as the Communicator of pair 18 (*B*), but it is interpreted differently by the respective Addressees. Arguably, Addressee 2 may have inferred from the Communicator's actions that she needed to rotate twice, similar to the strategy used by pair 21.

Movie S3 (A)
Movie S3 (B)
Movie S3 (C)
Movie S3 (D)




**Movie S4.** Interactive behaviors evoked during trials 30, 32, 46, and 50 of the communicative task by the same participant pair (pair 21). A communicative behavior can have different meanings in different trials, depending on the current conversational context of a pair. For instance, in trial 30, the Communicator uses an exit-point strategy to indicate the orientation of the Addressee's triangular token, leaving the relevant grid location along the direction where the triangular token needs to point (*A*). In trial 32 (and onward), the same player has started to use a wiggle strategy to indicate the target orientation of the triangle (*B*). In trial 46, the same player is presented (for the first time) with a goal configuration involving a triangle that points "outward." In this trial, the wiggle is absent (*C*). This absence is successfully interpreted by her Addressee as indicating an unusual orientation of the triangle. The success of this communicative interaction is even more remarkable given that in trial 30, the Communicator produced a similar behavior to mean a different goal configuration. In this pair of participants, the absence of a wiggle as a mark for an outward pointing triangle is used in a few more trials (e.g., trial 50) (*D*), until a different strategy is selected in later trials (not shown).

Movie S4 (A)
Movie S4 (B)
Movie S4 (C)
Movie S4 (D)




**Movie S5.** Interactive behaviors evoked during trials 9, 11, and 17 of the communicative task by the same pair of participants (pair 9). A particular problem type can induce different communicative behaviors in different trials, depending on the current conversational context of a pair. For instance, in trial 9, both participants' tokens are triangular, and the Communicator tries to convey to the Addressee her goal configuration by matching it with his own token (*A*). This strategy, however, does not apply to trial 11, where each player controls a differently shaped token, forcing them to negotiate a different strategy. In this case, the Communicator chooses to wiggle to indicate the orientation of the triangle, and the meaning of this behavior is understood by the Addressee (*B*). This shared symbol is also used in trial 17 (*C*), despite the fact that the problem presented in this trial is similar to the problem of trial 9 and that, in trial 9, a different communicative behavior was used (*A*).

Movie S5 (A)
Movie S5 (B)
Movie S5 (C)