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Research report

Mental state inference using visual control parameters

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Abstract

Although we can often infer the mental states of others by observing their actions, there are currently no computational models of this remarkable ability. Here we develop a computational model of mental state inference that builds upon a generic visuomanual feedback controller, and implements mental simulation and mental state inference functions using circuitry that subserves sensorimotor control. Our goal is (1) to show that control mechanisms developed for manual manipulation are readily endowed with visual and predictive processing capabilities and thus allows a natural extension to the understanding of movements performed by others; and (2) to give an explanation on how cortical regions, in particular the parietal and premotor cortices, may be involved in such dual mechanism. To analyze the model, we simulate tasks in which an observer watches an actor performing either a reaching or a grasping movement. The observer's goal is to estimate the 'mental state' of the actor: the goal of the reaching movement or the intention of the agent performing the grasping movement. We show that the motor modules of the observer can be used in a 'simulation mode' to infer the mental state of the actor. The simulations with different grasping and non-straight line reaching strategies show that the mental state inference model is applicable to complex movements. Moreover, we simulate deceptive reaching, where an actor imposes false beliefs about his own mental state on an observer. The simulations show that computational elements developed for sensorimotor control are effective in inferring the mental states of others. The parallels between the model and cortical organization of movement suggest that primates might have developed a similar resource utilization strategy for action understanding, and thus lead to testable predictions about the brain mechanisms of mental state inference.
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1. Introduction

Although 'mental state inference', more generally 'theory of mind', has been a recent topic of interest in cognitive neuroscience (see Refs. [4,9,26,28,83]), there are no computational models that go beyond conceptual arguments and none that offer testable predictions on the nature of mental state inference [27]. On the other hand, 'motor imagery' or 'mental simulation' has been widely studied by cognitive scientists, and recently by cognitive neuroscientists shedding light on the neural basis of motor imagery [12,47,48,61,66,67]. Our goal is to contribute to mental state inference and motor imagery research by developing a computational model that starts from a visuomanual control mechanism and can be extended into a mental simulation system allowing mental state inference, while conforming to human brain imaging and monkey neurophysiology data.

The first key observation for our proposal, that control mechanisms for movement generation can be used to make inferences about others' behavior, is that a goal-directed movement can be formulated as a feedback control problem. For example, reaching a target in space requires, at least,

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minimization of the distance between the hand and the target. Humans fixate certain landmarks critical for the control of grasping, such as where contact events take place, and the time when gaze exits a given landmark coincides with kinematic events at that landmark [44]. This suggests that humans monitor kinematic events to detect errors in execution. It is not clear to what extent the visual feedback is used during grasping, as there are contradictory results in the literature [10]. In primates, the exact form of the features extracted by the cerebral cortex for visual feedback control is not known. However, the parietal cortex appears to be involved in visuomotor aspects of manual manipulative movements [1,7,21,20,30,46,53,82,90]. The feedforward control, we assume, is a skill learned by self-observation of feedback-controlled movements, which involves inverse model learning (e.g. feedback error learning), and is not addressed in the current study (but see Refs. [52,92]). The parietal areas with specific connections to the frontal lobe mediate distinct sensorimotor transformations related to the control of hand, arm, eye or head movements and space perception. The activity of the fronto-parietal circuits is thought to control actions requiring spatial processing [72]. It is suggested that the premotor cortex may play a preferential role in sensory or context-dependent processing related to task performance, whereas motor cortex may be more involved in processing related to the purely motor aspects of task performance [77]. In addition, some premotor cortex neurons (mirror neurons) appear to be involved in both movement generation and also action understanding [29,70].

Our model structure is based on the hierarchical view [36] of primate visuomotor control with visual features being extracted by parietal cortex and used by the premotor cortex to generate high-level motor signals that drive lower motor centers thereby generating movement. The functional framework is developed based on mirror neuron findings from monkey and human brain imaging data, constrained by computational requirements. According to the model, action recognition is mediated by unconscious or implicit mental movement simulation that is implemented in the premotor cortex, which subserves mental state inference.

There exists considerable evidence that humans are endowed with a mental simulation capability mediated by the parietal and premotor cortices [31,48]. Chronometric studies suggest that viewers decide if the presented stimulus is a left or right hand, by engaging implicit motor imagery, a simulation that respects the rotational constraints of the observer's upper limbs [65]. In addition, humans use implicit mental simulation when asked to decide how they will grasp a handle appearing in a variety of orientations (over-hand vs. under-hand), and subjects' choices are in agreement with the grips chosen during actual grasping [45]. Furthermore, experiments utilizing PET imaging have shown that similar to actual and imagined movements, premotor, parietal and cerebellar regions (but not primary somatosensory and motor cortices) are strongly activated during implicit mental simulation [66] supporting our model. Although in the current study, the utilization of mental imagery for mental state inference was the emphasis, mental simulation mechanisms can also play an important role in motor planning as suggested by the Prospective Action Model (PAM) in which movement alternatives are simulated and evaluated to determine the most biomechanically efficient movement for execution [45,48]. Note that the mental simulation we are referring to is continuous (analog) in nature, and is a different process than 'visual mental rotation' [11,40,78] that does not involve motor imagery.

For different tasks, a multiplicity of specialized controllers may be acquired. A structure similar to the MOSAIC model, a modular adaptive controller, can be involved in such task learning [39,95]. In this study, we investigate the mechanisms that allow *exploitation* of motor circuits for mental state inference rather than learning. As will be elaborated later, the key to this mechanism is the existence of *internal models*. Although theoretically perfect control does not necessarily require any identifiable internal models [57], current evidence suggests that the central nervous system uses internal models for transforming sensory stimuli into movement; i.e. in planning, control and learning [51]. Internal models that predict the sensory consequences of a motor command are known as *forward models* as they can be used to predict how the motor system's state changes in response to a given motor command [94,95]. In a more general sense, a forward model is a mechanism to predict a future event, given the set of inputs such as the motor command and current state that can affect the system's future. Mehta and Schaal give an excellent review of possible control schemes for the human brain with and without internal models and show with their experimental paradigm that visuomotor control involves at least one forward model [57]. The role of forward models in *control* is twofold: eliminating sensory processing delays [59,93] and mediating inverse model learning for establishing a feedforward control strategy [14]. Our model extends the function of the forward model beyond motor control, highlighting the key role played by the forward model in decoupling the mental movement execution from the actual one.

2. Methods

We now introduce our model by describing a generic visual control circuit and then show how it can be adapted into a mental simulation and mental state inference circuit. In Discussion, we elaborate on the connection between the cortical movement and action recognition areas and the model structures, which together with simulation results lead to predictions that can be tested experimentally.

2.1. Generic visual feedback circuit for goal-directed movements

Based on experiments on goal-directed hand movements, we propose the following neural processing steps. The

parietal cortex extracts visual features relevant for the control of a particular goal-directed action (X, called the control variable) and relays this information to the premotor cortex. For example, by taking X as the distance between the index finger and a given target location, the circuit drives a reaching movement. On the other hand, if we take X as the sum of the distance between index finger and its target surface, and the thumb and its target surface, we have a circuit for grasping [80,81]. The premotor cortex computes the motor signals to match the parietal cortex output (X) to the desired neural code (X_{des}) relayed by prefrontal cortex. We assume that premotor cortex is an adaptive circuit that outputs movement parameters (e.g. desired change in body configuration) to achieve the goals represented by the prefrontal and parietal cortices. The 'desired change' generated by the premotor cortex is then relayed to the primary motor cortex and spinal cord for execution (Fig. 1). We acknowledge the involvement of the basal ganglia and the cerebellum in learning and dynamics control but do not include them in the model [33,43,50,76,92]. Although we did not simulate the dynamics and the delay—hence did not need a complex forward model, we assume that the sensory forward model (FM) (Fig. 1) helps feedback control of movement by eliminating delays in sensory feedback by providing future sensory signals to the premotor cortex. In general, the proposed FM needs to learn the composite mapping of the dynamics controller, the controlled body and the control variable computation and thus needs to access more resources than we have simulated (e.g. dynamics state of the body). Kinematics and dynamics transformations of high degrees-of-freedom mechanical system (humanoid robots) can be successfully learned with recent learning

architectures in an online fashion [86], thus we believe the brain could acquire such a powerful FM as suggested elsewhere [57,59]. Note that at this level, we define the forward model in functional terms. In a biological system, multiple cortical structures may be involved in implementing such a composite forward model (see Discussion).

The model architecture proposed is orthogonal to whether a multiplicity of parallel circuits or a circuit with different instantiation parameters allows deployment of different control strategies. Depending on the intentions of an organism (e.g. grasping, tearing, etc.), the functionality of the parietal and premotor cortices is 'switched' or 'modulated' by the prefrontal cortex providing the operational space (extrinsic, kinematic-based) signals and the visual control servo required for the desired task execution. Thus, the parietal and premotor cortices form a set of task-specific operational space control mechanisms, which are engaged according to prefrontal influences. Our view is in accordance with the experimental findings that control strategies for goal-directed movements differ according to the task in which the subject is involved [87].

2.2. Exploitation of control variables and mental state inference

The second key observation that is crucial for the model is that the time course of a control variable (e.g. distance) extracted for visual feedback control of movement can be readily used to recognize others' movements if the variable is invariant under translation and rotation. The invariance can be embedded in the parietal processing (i.e. built in the control variable) or an explicit coordinate transformation
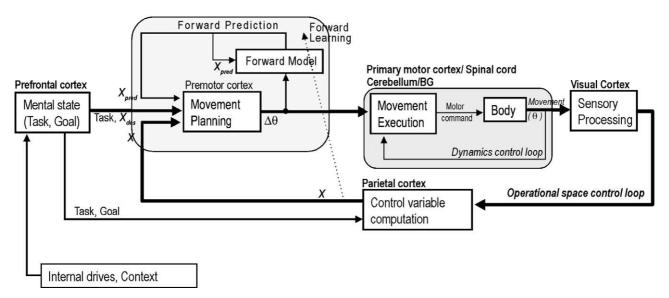

Fig. 1. The visual feedback control mechanism proposed for goal directed actions is shown. The context and internal drives culminate in a mental state, 'wanting to do something' in prefrontal cortex which modulates parietal cortex for extraction of the required control variables to fulfil the goal. Premotor cortex (movement planning) receives signals from parietal cortex and prefrontal cortex, and computes the movement signals required to achieve $X_{des}=X$. The movement execution (lower motor areas: the primary motor cortex, spinal cord, the basal ganglia and the cerebellum) implements instructions relayed by the premotor cortex.

circuit can preprocess sensory inputs and relay the output to the parietal cortex. For example, the angle between two planes in space is invariant under translation and rotation. Along these lines, it has been shown that it is possible to recognize grasping movements and classify them into different grip types [64].

Thus, we propose that neural circuits evolved for goal-directed manipulation skills (e.g. breaking a nut, holding a cup) not only provide dexterity in task execution but also mediate understanding of another's intentions if used in a mental simulation mode. The key element for this *extended* function is the dual role of the FM that is mediated by inhibitory mechanisms. During *task execution*, the parietal cortex, the premotor cortex and FM implement a visuomanual servo, where the FM compensates for visual feedback delays. During mental state inference, the FM is utilized for creating imaginary parietal signals based on the current mental state estimate, which is decoupled from the action of the observer, while the parietal cortex processes the visual stimuli created by the observed movement. In brief, behaviors are generated by the actor's motor control system which is internally parameterized by intention (not visible to an observer). The observer, by simulating the motor control system with an initial estimate of this internal parameter, can compare its simulated output with the observed act, generating an error measure that allows updating of the observer's internal parameter until there is a good match between the actor's behavior and the observer's prediction. In the simulations we present in this paper, we analyze two kinds of mental state estimate correction. The first method is applicable only when there is a discrete set of possible mental states. This method simply finds the most likely estimate by rejecting mental state hypotheses that lead to larger errors. The second correction method is based on stochastic hill climbing, and it finds an approximate gradient in the (continuous) mental state space using stochastic 'mental state perturbations'.

Fig. 2 illustrates the extension of the visuomanual control circuit presented in Fig. 1 into a mental state inference system. This extension represents a *conceptual model of primate exaptation* (the utilization of a structure for a function other than that for which it was developed through natural selection) of the sensory forward model (FM) introduced in Fig. 1.

The basic processing steps carried out in the model can be written as a cascade of transformations, with some of the transformations depending on the current (and hypothesized) mental state of the system, which we index by j (and i). The transformations and variables are:

MP   movement planner
DC   movement execution (dynamic controller)
FD   body forward dynamics
CV   control variable computation
FM   forward model
X_j^n actual control variable for mental state j at time n

$X_{j,\text{pred}}^n$ predicted value of the control variable at time n for mental state j

$X_{j,\text{observed}}^n$ observed control variable for mental state j at time n

delay   time *delay* to convert from movement plan to sense-controlled variable

θ_j^n state of the body

$\Delta\theta_j^n$ desired change in the body state at time step n.

When the model is in the actor mode with mental state j:

(1) $X_{j,\text{pred}}^n = \text{FM}_j(\Delta\theta_j^{n-1}, X_{j,\text{pred}}^{n-1})$	The forward model predicts the control variable for the next time step and cancels out the delay involved in CV.
(2) $\Delta\theta_j^n = \text{MP}_j(X_{j,\text{pred}}^n, X_j^{n-\text{delay}})$	The motor planning generates movement signals.
(3) $\theta_j^{n+1} = \text{FD}(\text{DC}_j(\Delta\theta_j^n + \theta_j^{n-1}, \theta_j^{n-1}))$	Dynamics controller fulfills $\theta_j^{n+1} \cong \theta_j^n + \Delta\theta_j^n$.
(4) $X_j^{n+1} = \text{CV}_j(\theta_j^{n+1})$	The result of the change in the hand–object relation is captured in control variable computation which is approximated by FM (step 1), completing the operational space feedback loop.

When the model is in the observer mode with the hypothesis of i as the actor's mental state

(1) $X_{i,\text{observed}}^n = \text{CV}_i(\text{Actor})$	The control variable from the observation of the actor is extracted using CV of the observer but directed to the movement of the actor.
(2) Mental simulation ($m=1,\dots,n$)	
(a) $X_{i,\text{pred}}^m = \text{FM}_i(\Delta\theta_i^{m-1}, X_{i,\text{pred}}^{m-1})$	Predict the control variable of the next time step.
(b) $\Delta\theta_i^m = \text{MP}_i(X_{i,\text{pred}}^m)$	Generate movement signal to be used by step (2a).

Then, the task of mental state inference in the observer is to search over mental states (i) that will produce minimal mismatch between $[X_{i,\text{observed}}^1, X_{i,\text{observed}}^2, \dots, X_{i,\text{observed}}^n]$ and $[X_{i,\text{pred}}^1, X_{i,\text{pred}}^2, \dots, X_{i,\text{pred}}^n]$. The mental simulation equations (2a and 2b) do not involve any movement and visual processing, thus can be executed very rapidly.

Note that our simulations analyzed the observer; the actor was implemented without delay and dynamics. In general, the dynamics require the θ in the above equations to include the time derivate (i.e. $\theta \triangleq (\theta, \dot{\theta})$, and the dynamics control loop (actor case step 3) can be run at a higher rate than the operational space control loop, or alternatively, it can be replaced with an inverse dynamics controller. Another issue is that the forward prediction must be initialized to match the real control variable prior to operation. This initialization can be accomplished by having no movement for a period of *delay* or more (i.e. $X_{j,\text{pred}}^{0,1,\dots,\text{delay}} = X_j^0$ and $\Delta\theta_{j,\text{pred}}^{0,1,\dots,\text{delay}} = 0$).

To give a concrete example, we use a reaching task and trace the functioning of the model (see Fig. 2). Imagine an
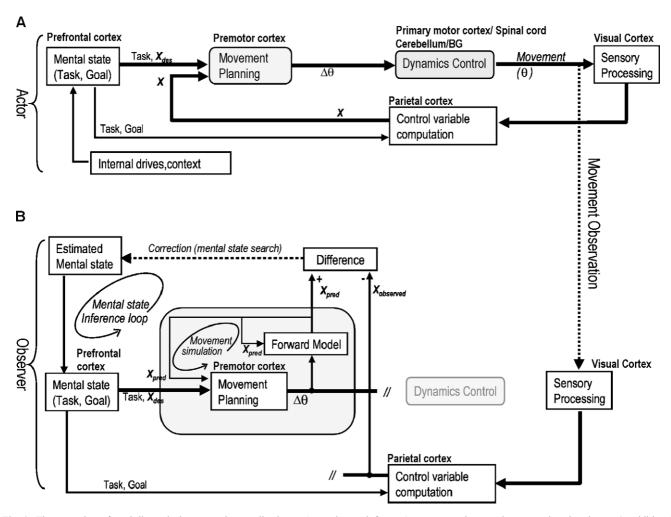
Fig. 2. The extension of goal-directed visuomanual controller into a 'mental state inference' system can be seen by comparing the observer's additional circuitry (lower part) to the actor's. The slashes (//) indicate inhibition or blockade of motor execution. The difference module computes the difference between the control variables of the simulated movement (based on the current estimate of the mental state of the actor) and the actual observed movement.

actor being asked to freely select and reach to one of a set of targets in space. The observer's task is to guess to which target the actor is reaching as soon as it can. Given this scenario, we first describe what happens in our model from the actor's viewpoint then we elaborate on observer's mental state estimation.

The type of movement (i.e. reaching) and its goal constitute the mental state of the actor. During movement, Parietal Cortex computes the distance between the target and the hand while Premotor Cortex generates target joint angles to reduce the distance information relayed by Parietal Cortex. Low-level motor centers convert the output of Premotor Cortex to neural signals that drive muscles causing movement, which in turn modifies the parietal distance signal. The output of Premotor Cortex is also relayed to the FM to predict the sensory outcome that is integrated with parietal output by premotor cortex to compensate for delays and temporary interruptions in the sensory processing (e.g. due to occlusion). The acquisition of the FM is mediated by the outputs of Premotor Cortex and parietal cortex, which we assume has taken place

already prior to the reaching task. The visual feedback loop continues until the desired zero-distance is achieved, driving the hand towards the target specified by the mental state of the actor.

The observer's aim is to infer the goal of the actor's movement and starts with some hypothesis in the estimated mental state. The premotor cortex does not receive input from the parietal cortex and instead relies only on the FM output to generate movement signals as observer's parietal cortex is engaged in computing the hand–target distance pertaining to actor's movement. The FM receives the output from the premotor cortex and computes the predicted outcome (X_{pred}) implementing the mental simulation loop. Output of the observer's premotor cortex is inhibited so that the mental simulation does not trigger overt movement. The broken links (//) in Fig. 2 indicate the switch between the overt movement and simulated movement mode. The difference module compares the stream of sensory signals based on real movement (X) and mentally simulated movement (X_{pred}), and produces an error signal that is used for modifying the current hypothesis about the actor's goal.

In the following sections, we present the simulation environment and the experimental settings. In brief, the simulation experiments (SE) conducted are: the straight-line reaching simulations (SE1), where it is shown that the model can perform mental state inference with stochastic gradient descent in a continuous mental state; the spiral reaching simulations (SE2), where it is shown that the mental state inference model is not limited to 'easy to predict' mental state inference tasks and can be generalized to complex goal-directed movements as long as the control is specified with respect to the goal; and the deceptive reaching simulations (SE3 and SE4), aim at showing the situation where the actor and observer have different movement strategies. In this case, the mental state representations of the actor and the observer can be very different. Finally, a tool-use simulation (SE5) shows that the mental state inference is applicable to grasping movements and a parallel implementation can be used to generate a probability distribution over the set of possible intentions afforded by the context.

2.3. Simulation environment

We simulated two experimental setups. The first one involves two agents sitting and facing a board on which there are several target locations. As one agent reaches for a target, the other's task is to guess the first's intended target as rapidly as possible. The second setup involves a tool (hammer) that can be grasped in several ways. The observing agent watches another agent grab the tool and has to infer the agent's intention. In the former case, we modeled the arm as a two-link kinematics chain, whereas in the tool-use case, the hand was also included as the end-effector. The hand/arm is modeled to have 3DOF joints at the shoulder to mimic a human shoulder ball joint and 1DOF joint in the elbow for lower arm extension/flexion movements (see Fig. 3). The wrist is modeled to have 3DOFs to account for extension/flexion, pronation/supina-

tion, and ulnar and radial deviation movements of the hand. Each finger has 2DOF whereas the thumb has 4DOF. The finger and thumb joints are used to implement an open loop enclosure of fingers at hand–object contact. In each case, the actor and observer models 'know' how to perform reaching and grasping movements, implementing the control mechanism shown in Fig. 1.

2.4. Task implementations

Since the dynamics of the arms are not modeled, the dynamics control box shown in Fig. 1 is the identity mapping for the simulations presented in this paper. The task of the movement-planning module (the premotor cortex) is, therefore, to plan a trajectory in three-dimensional space. The parietal cortex computes the control variables required for task execution and observation. In general, the forward model is a neural network that learns a goal-directed transformation (e.g. orientation with respect to an external reference) of the operational space forward dynamics of the controlled body and the controller. In this simulation for computational convenience, we use the exact mapping instead of a neural network. The FM module receives the joint angles as input and output (*distance*) for reaching and (*distance, orientation difference*) for tool-use (grasping).

2.4.1. Reaching task implementations

In the first set of reaching simulations (continuous mental state space), the mental state of each agent is modeled as the three-dimensional coordinate of a target on the board plane (Fig. 4A). In the second set of reaching simulations (discrete mental state space), the mental state is modeled as the identity of the reach target (an integer number indicating a target).

In the straight reaching case, agents produced a straight-line hand path to reach a target. For spiral reaching, we relaxed the straight path requirement, allowing spiral paths
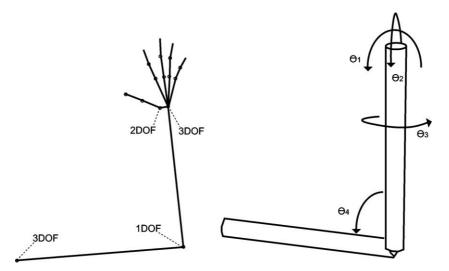

Fig. 3. The arm/hand model has 19 DOFs (left). Zero posture of the arm/hand and the positive rotations of the arm are shown (right).
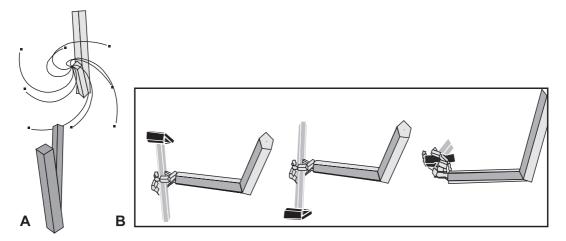
Fig. 4. On the left (A), the reaching task simulation setup is shown (the spiral reaching paths for the eight targets are also shown). The demonstrator model reaches for one of the targets (small squares) while the observer model tries to infer demonstrator's goal by 'mental simulation'. On the right (B), three intentions of grabbing a hammer are shown. Left to right: hammering a nail (nailing task), pulling off a nail (prying task) and putting the hammer away (holding task).

parameterized by the current position of the end-effector. Finally, the deceptive reaching involved selection of a 'fake' target, which altered the reaching movement kinematics to deliberately deceive an observer (see Appendix A for details). In reaching movements, to account for possible inaccuracies during perception, zero-mean Gaussian noise with a variance of 25 was added to the parietal distance computation. At the onset of movement, the end-effector–target distance was 700–800 units depending on the target, and inter-target distance was 350 units vertically and horizontally.

2.4.2. Tool-use (grasping) movement implementations

The tool-use experiment is set up with a hammer and two agents that can grasp the hammer with three different intentions. When a hammer is grasped by the handle so that the metal head points upwards at the end of movement is considered as an intention of driving a nail (*nailing task*) while a grasping movement that results the metal head pointing down is considered as an intention of pulling out a nail (*prying task*). Finally, grasping the hammer merely from its metal head is considered as an intention of putting it away (*holding task*). The grasping movements mentioned are illustrated in Fig. 4B. The tool-use experiment modeled mental state as the intention of grasping the hammer (holding, nailing or prying a nail). The grasping movements prior to driving and prying a nail require differential alignment of the hand and the thumb. The *knuckle vector* (the vector pointing away from the little finger knuckle towards the index finger knuckle) must point towards the metal head of the hammer prior to nailing while it has to point just opposite prior to pulling out a nail. We have assumed that a hammer is approximately grabbed from the center of the handle in these two grasps. The final grasp indicative of holding rather than driving or prying a nail, is modeled as the hand's bottom approach towards the center of the metal head while maintaining a vertical approach to

the hammer plane (plane spanned by the handle and the metal head). Appendix A provides details of these grasps.

2.5. Mental state inference implementation

As the control variables described for reaching and grasping movements are defined in extrinsic space with respect to target, the need for an explicit coordinate transformation circuit for mental state inference is eliminated. Hence, the history of the control variables can be used to compare two movements (i.e. simulated and real movements). For example, straight reaching requires the control of *distance* between the end-effector and the target. In general, the details of how the distance is reduced to zero depend on an agent's movement strategy as well as the agent's intrinsic and extrinsic properties. With the assumption that both agents have similar mechanisms, we expect (in spite the variations in the agents) the different goals will yield different *distance trajectories*, so that mental state correction can be performed using mentally simulated movements. Similarly, for hammer grasping, we expect that the *distance* and *orientation difference* trajectories can be used to infer the intention of an agent grasping a hammer. Note that although object centered formulation of the control problem avoids explicit coordinate transformation, in general, some normalization might be required, as is the case for distance (but not for orientation difference). Distance normalization can easily be based on an initial estimate of the distance of actor's hand to a target. In the simulations presented here, the actor and the observer were placed equidistant from the target board eliminating the need for distance normalization.

If an observer model 'knows' the possible mental states (goals) of an actor as discrete entities, then it can perform an exhaustive search in the mental state space. However, if the number of possible mental states (and related targets) is infinite, or the targets are not visible to the observer, then a

different search strategy must be applied. From a computational point of view, the mental state correction requires the 'control variable differences' (the difference box Fig. 2) to be converted into 'mental state space adjustments'. Although the current difference module implementation does not perform scaling or any other advanced manipulations to compare two input time series, the difference computation involves an integral over sensory signals produced during a feedback loop. Therefore, it is not trivial to formulate a general deterministic gradient descent algorithm. Nevertheless, we can perform stochastic 'hill climbing' in the error space. We have implemented both the exhaustive and the stochastic gradient search methods, for which we present algorithms, assuming that parietal cortex (feature extraction/control variable) processing is serial (i.e. it can process the visual input related to a single target at a time). The parallel version is straightforward and not included here.

Algorithm. Exhaustive mental state search (for a mental state space with M discrete elements)

(1) **Initialize**: Set T_k and S_k to empty sequence ($T_k=S_k=[]$). Here T_k and S_k represent sequences of observed and mentally simulated vectors of visual control variables extracted under the mental state k.
(2) Repeat steps a–e from movement onset to movement end.
  (a) Pick next possible mental state (j) (which can be thought of as an index to the possible target the actor is reaching to).
  (b) **Observe**: extract the relevant control variables based on the hypothesized mental state (j), x_j^i and add to T_j ($T_j=[T_j,x_j^i]$). Here the superscript notation i indicates that the collected data was placed in ith position in the visual control variable sequence.
  (c) **Simulate**: mentally simulate movement with mental state j while storing the simulated control variables x_j in S_j ($S_j=[x_j^0,x_j^1,\ldots,x_j^N]$, where N is the number of control variables collected during movement observation).
  (d) **Compare**: compute the discounted difference between T_j and S_j, where N is the length of T_j and S_j.
$$D_N=\frac{(1-\gamma)}{(1-\gamma^{N+1})}\sum_{i=0}^{N}\left(x_{\text{sim}}^i-x^i\right)^T\mathbf{W}\left(x_{\text{sim}}^i-x^i\right)\gamma^{N-i},$$
where $x_{\text{sim}}^i\in S_j$ and $x^i\in T_j$ and $\mathbf{W}$ is a diagonal matrix normalizing components of x^i, and γ is the discount factor.
  (e) If D_N is smallest so far, set $j_{\text{min}}=j$.
(3) **Return**: j_{min} (observer infers that j_{min} is the actor's mental state).

In general, a mental space may not be indexed and finite and thus the above algorithm cannot be applicable. The following algorithm assumes that the mental space is a continuous metric space (e.g. in the reaching task, the mental state is modeled as the two-dimensional open set defined by the board borders.)

Algorithm. Stochastic gradient descent mental state search (for a continuous mental state space)

(1) **Initialize**: Set A to an initial random mental state guess; set MaxIter to a positive integer (e.g. 20 for reaching task); set $D_{\text{last}}=1e20$ (arbitrarily large number).
(2) Repeat a–c from movement onset to movement end.
  (a) **Observe**: Add actor's current kinematics (e.g. end-effector position) in sequence K.
  (b) Loop MaxIter times.
    (i) Generate a random perturbation ΔA.
    (ii) Apply the perturbation to A: $A=A+\Delta A$.
    (iii) **Recompute**: the vector of control variables for mental state A using K and store in the sequence T_A ($T_A=[x^0,x,\ldots,x^N]$). Here N is the length of K, and the superscript notation i indicates that the data was placed in ith position in T_A.
    (iv) **Simulate**: mentally simulate movement for mental state A and store the vector of control variables generated during imagery movement in S_A.
    (v) **Compare**: $D_N=\frac{(1-\gamma)}{(1-\gamma^{N+1})}\sum_{i=0}^{N}\left(x_{\text{sim}}^i-x^i\right)^T\mathbf{W}\left(x_{\text{sim}}^i-x^i\right)\gamma^{N-i}$, where $x_{\text{sim}}^i\in S_A$ and $x^i\in T_A$ and $\mathbf{W}$ is a diagonal matrix normalizing components of x^i, and γ is the discount factor and N is the size of T_A and S_A.
    (vi) If $D_{\text{last}}<D_N$ then undo with %20 penalty: $A=A-1.2\Delta A$ and go to step i.
    (vii) If rand<0.1 go to step i (even if the perturbation was good, with small probability make a random move).
    (viii) Go to step ii (if the perturbation was good, use it once more).
(3) **Return**: A (observer infers that A is the actor's mental state).

The discount factor for difference computation (D_N) was chosen as $\gamma=0.9$ for all the simulations. The parameter γ allows forgetting of the early (and ambiguous due to noise) portions of the movement observation. The normalization matrix $\mathbf{W}$ was unit diagonal matrix in the reaching experiments and diag(0.7,0.3) in the tool-use grasping experiments. In general, $\mathbf{W}$ controls the relative weight of features appearing in the difference computation (e.g. distance and orientation difference).

The exhaustive search algorithm implements a *serial parietal cortex* that can 'attend' a single target at a time where the potential mental states are iterated serially keeping record of the best so far. For tool-use simulations, the parallel version of the exhaustive search algorithm is

used which does not cycle through the potential states but computes all at the same time in a parallel fashion. The output of the parallel difference computation (D_N) is then converted into beliefs using the softmax function:

$$p(A_i | observation) = \mathrm{e}^{-20D_{Ni}^i} \left/ \sum_{j=1}^{M} \mathrm{e}^{-20D_{Ni}^j} \right.$$

where A_i represents one of M mental states.

Certainly, a circuit capable of parallel processing computes faster; however, the requirement of feature extraction from multiple visual targets simultaneously (i.e. control variable computation for multiple goals) raises the question of how many visual targets a biological agent is able to monitor at the same time. This issue is related to *attention* and capacity *of working memory*, which we do not elaborate here as it is beyond the scope of this paper.

3. Results

We first present simulation experiments of straight line (SE1) and spiral reaching (SE2) that use gradient search for mental state inference (see Methods for details of the simulations) where the actor and the observer have similar movement strategies. In these cases, the mental state space was modeled as the set of points on a bounded plane segment (the 'board'). The actor reached for fixed targets on the board; however, the observer was not aware of the fixed targets. Therefore, the observer used a continuous mental state (target location on the board) search to infer the goal of the movement.

3.1. SE1: straight-line reaching actor vs. straight-line reaching observer (continuous mental state search)

In this simulation, there are eight targets placed on the board as shown in Fig. 4A (the center target is not used), which are only visible to the actor.

Each target is equidistant from its vertical and horizontal neighbors (350 units). The mental state search requires an initial guess of the actor's mental state. In general, the initial guess can be guided by the context or other cues. Here we initialized the estimated mental state as the center of the target board. Fig. 5A shows the trajectory of the mental state of the actor that represents the goal location (gray line) which jumps from the initial central location to the target, and the predicted target of the observer (black trace). Although the estimates of mental states have variability (arising from noise on the visual feedback and the stochastic nature of the search), the trajectories arrive at the correct mental state. Fig. 5B illustrates the temporal aspect of the mental state search, showing the distance between the observer's estimate of the actor's goal and the actual goal of the actor as a function of simulation time. The target of the movement

can be reliably estimated midway through the movement. Note that here we present typical convergence patterns. The speed of correct inference depends on the ambiguity of movement patterns, the noise level in the control variable extraction and the number of cycles the stochastic gradient descent search algorithm is run per observation data point (see Methods for details). Although simple, these simulations show that the time course of the control variable used in movement generation (distance) can be used to assess the similarity of a mentally simulated movement and observed movement.

3.2. SE2: spiral reaching actor vs. spiral reaching observer (continuous mental state search)

Although reaching is not a very rich behavior in terms of goal-directedness, a general goal-directed reach can be defined in the reference frame of a target. In this simulation experiment, we show that the capacity of mental state inference model is not limited to simple straight-line reaching but can be generalized to general goal-directed movements. We implement a spiral reaching movement where the path followed by the actor is defined with respect to the board rather than specified egocentrically. Intuitively, this means that the turns of the spiral are not specified as, say, left to right but as from target 2 towards target 1 (see Methods for more details). Fig. 6A shows the successful mental state search patterns when the observer and actor use the spiral reaching strategy (see Fig. 4A). As in all gradient methods, the search suffers from local minima. Compared to the straight line reaching, the spiral reaching presents more local minima and more susceptibility to noise. The central panel in Fig. 6B shows the best convergence and worst convergence patterns normalized and averaged over eight targets; in the worst case, the correct inference is delayed. In spite of the local minima, our simulations show that the time course of control variables used in movement generation can be used to assess the similarity of a mentally simulated movement and observed movement even if the set of possible targets is unknown. Our simulations also showed that a naive straight-line reaching observer could not estimate the target of an actor's goal when the actor performed a spiral reaching (or vice versa) since the mental simulation was very different from actor's movement. These simulation results are not shown for they are similar to the results for deceptive actor vs. naive observer case, which we present next.

3.3. SE3: deceptive reaching actor vs. straight-line reaching observer (discrete mental state search)

Next, we present a series of simulations (SE3, SE4) using exhaustive search method where the actor and the observer can have different movement strategies (straight line and deceptive reaching). In these simulation experiments, the mental state space is modeled as finite (i.e. the

reach targets are fixed locations on the board) as illustrated in Fig. 4A.

As a first step for information transfer between agents, we introduced a reaching strategy by a 'deceptive' actor who initially chooses a fake target to aim for with the intention of deliberately forming a false belief (mental state estimate of his) in the observer's mind. We expected that the first portion of the deceptive actor's movement would fool a 'naive' observer who uses a straight-line reaching strategy until the later portions of the movement. The simulation results showed that the 'naive' observer failed to estimate the goal of the actor's reach since a straight-line reaching strategy controls only the distance to a (real) target. In other words, the mental state of a naive observer was lacking an important component, the possibility of the existence of a fake target. By using a board with four targets, we can examine all possible deception scenarios: when the actor chooses one of four real goals and therefore has three possible fake goals

(leading to 12 possible scenarios). The movements arising from all possible mental states of the deceptive actor are depicted in the sub-panels in Fig. 7 (dashed line real target; dotted line fake target). The vertical axis indicates the target, whereas the horizontal axis represents simulation cycles from movement onset to movement completion. The belief of the observer about the actor's reaching goal is super-imposed as a solid line showing that the actor was deceived during the deceptive movement observation (the overlap of the solid and dotted lines).

3.4. SE4: deceptive reaching actor vs. deceptive reaching observer (discrete mental state search)

To verify that SE3 is indeed a deception case, we checked the goal estimation capability of an observer with the same deceptive strategy as the actor. Thus, the observer and actor had the same mental state space representation and
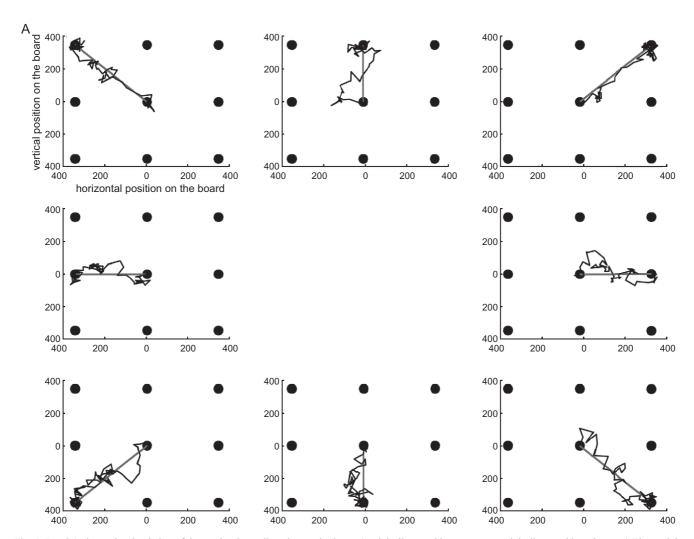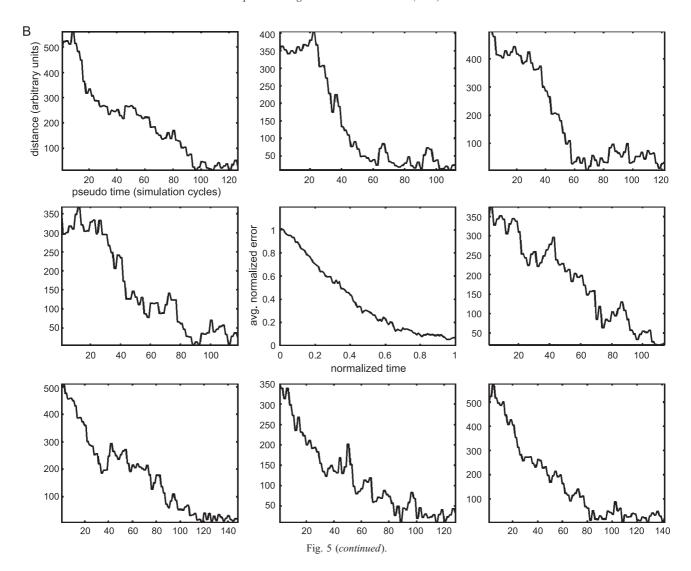

Fig. 5. Panel A shows the simulation of the stochastic gradient descent is shown (straight-line reaching actor vs. straight-line reaching observer.) The straight line in each sub-panel indicates the actual goal of the actor. The black traces show the prediction of the observer. The initial estimate of the observer at the movement onset of the actor is taken as the center of the board. Panel B shows the distance of the estimated target to the real target of the actor as a temporal plot. In addition, the center plot (in Panel B) shows the error as normalized and averaged over the eight trials.

Fig. 5 (*continued*).

therefore the mental state search of the observer involved finding out the fake target as well as the real target. The result of this simulation set is shown in Fig. 8 with the same conventions as in Fig. 7, except this time we used a six-target board to make the goal inference harder. The movements get more ambiguous with more targets because the trajectory for each movement becomes closer; hence, the effect of the modeled noise becomes more severe (see Methods). Nevertheless, the observer of this simulation can correctly estimate the mental state of the actor and thus infer the goal of his movement much earlier than the naive observer of previous simulation experiments (SE3).

3.5. SE5: tool-use simulations

The last simulation experiment (SE5) involves grasping where the mental state is modeled as the intention of grasping a hammer, either driving a nail, prying a nail or holding the hammer to put it away (Fig. 4B). The intention of an actor determines what policy will be used to control the distance and orientation of the hand with respect to the hammer to provide a successful grasp. One of the important points that we did not emphasize in the reaching simulations was what the parietal cortices of the agent and the observer were computing during control and observation. In fact, when the deceptive actor was generating a deceptive reaching, its parietal cortex was computing the distance to both fake and real targets whereas the naive observer was computing a single distance for mentally simulating the movement. Since various mental states may require different control mechanisms, the control variables that need to be computed depend on the current estimate or 'hypothesis' of an observer. We present the tool-use simulation results using a scheme to emphasize this fact as follows. We construct a time-varying (mental simulation)×(observation) matrix to understand the full dynamics of the observer (Fig. 9). The rows of the matrix represent the intention of the actor: (holding, nailing, prying). The columns represent the possible beliefs of the observer: (holding, hammering, prying). Then each cell is used to show the similarity between mentally simulated movement and the observed movement as a function of simulation time from movement onset to movement end.

The similarity between observed and mentally simulated control variables are not directly compared to find the most likely mental state (as was case for reaching simulations) but instead converted into a set of probabilities (beliefs). Therefore, at any time step, each row sums to 1. The convergence to unity of the beliefs along the diagonal plots indicates that the observer could infer the mental state of the actor soon after the movement onset.

4. Discussion

4.1. General

The model presented an explicit account of how mental simulation and mental state inference loops can be built over existing visual feedback control mechanisms, mediating the understanding of the meanings of others' actions. The key ingredients for the reutilization of motor circuits for

perception is the existence of *forward models* that predict the sensory consequences of movement, and the *goal-directness* of the motor control policy. Our simulations showed that with these key ingredients, appropriate movement simulation and mental state search mechanisms enable mental state inference. Although similar views have been put forward by several researchers [4,28], to our knowledge, our study is the first computational approach to mental state inference and theory of mind, respecting the existing cognitive neuroscience findings.

The functional equivalence between action generation and action perception has gained considerable attention by the expanding human brain imaging studies [37]. These studies showed that motor regions become active for both action execution and observation, switching their function (e.g. Refs. [5,6,13,34,38,63,71]). One functional explanation of this dual activation is that during perception a copy of a motor schema is instantiated (see Refs. [2,3]) in motor centers to be used for action understanding. Although this
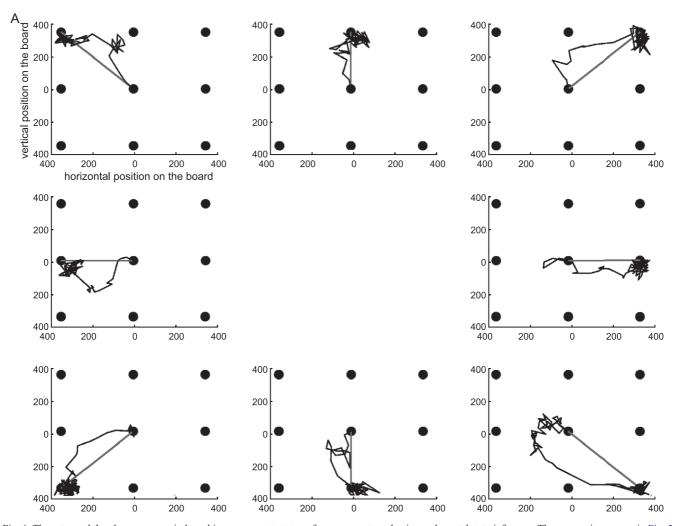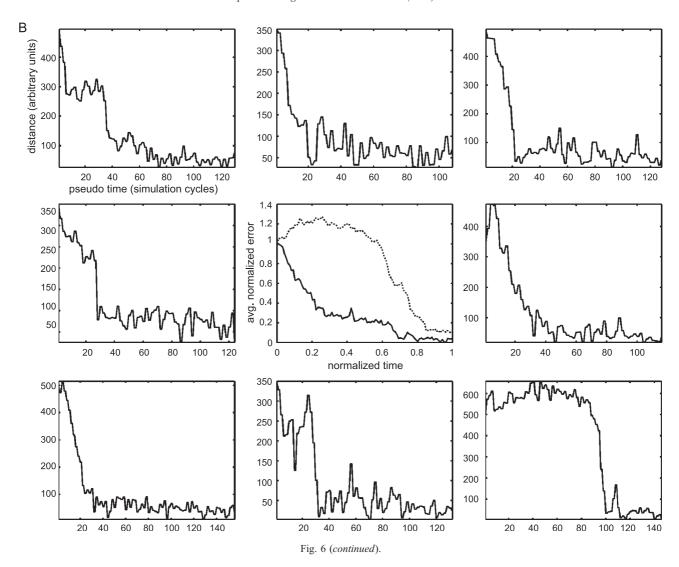

Fig. 6. The actor and the observer use spiral reaching movement strategy for movement production and mental state inference. The conventions are as in Fig. 5 (panel A: spatial solution path; panel B: temporal error plot) except that the center plot in panel B shows also the average normalized error for those trials where mental state search converged very slowly (dotted curve).

Fig. 6 (*continued*).

view is functionally attractive, there is no convincing explanation of how this could be implemented in the brain. The other alternative is to reuse the very same brain circuits for both execution and observation, but switch the inputs and outputs according to the task (i.e. motor control or action understanding.) It is agreed that the descending motor output to muscles must be inhibited during action observation. However, there are no studies on how and where the input switching occurs in the brain. From a computational perspective, switching is a complex task if it is to occur downstream in motor control since most motor circuits operate in intrinsic parameters such as joint angles, muscle activities, etc. During perception, these values pertaining to the actor have to be estimated accurately and channeled to observer's motor circuits so that a reuse of motor system is possible.

Our model predicts that the switching must occur at visual processing areas where the visual control parameters are extracted in a goal-directed manner (e.g. in the parietal cortex). Since the motor circuits are used only for mental simulation, the problem of input switching at the motor level does not occur in the model. The prediction is biologically plausible because visual attention readily allows mechanism that controls input switching for execution and observation. When human subjects are engaged in grasping, the gaze is directed towards contact targets on the object surface while the hand follows the fixation point suggesting that eye movements are part of motor planning [44]. The same pattern of eye fixations emerges when subjects merely observe a demonstrator performs the same manipulation [22]. In other words, the eye–hand coordination with *respect to the object* being manipulated is identical regardless of whether the task is executed or just observed during a demonstrator's execution. Notice that the 'hand' here is a pragmatic hand and it does not matter whether it belongs to the actor or the observer. Our model also assumes pragmatic feature extraction within the parietal cortex. During execution, visual processing is engaged in extracting control variable(s) based on the object and the controlled hand, while during observation, the control variables(s) extracted are based on actor's hand rather than the observer's.
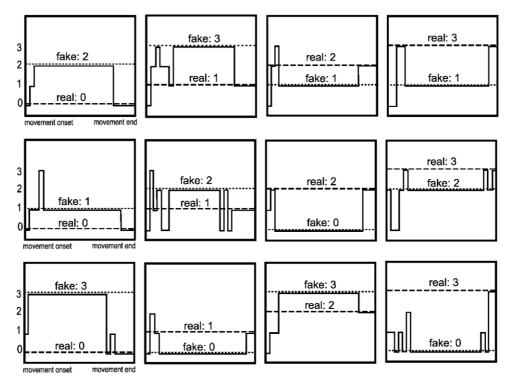
Fig. 7. Four-target (0, 1, 2, 3) board is used to show the goal estimate of the observer in response to all possible mental states of the actor. The dashed horizontal line in each panel represents the 'real' target, whereas the dotted line represents the 'fake' target. The observer's belief about the actor's goal is shown by solid line. The horizontal axis represents simulation cycles starting from movement onset to movement completion. The vertical axis indicates the targets (the vertical ordering has no spatial meaning on the target board.).

4.2. The mental state inference model and pretence as the precursor of theory of mind

A normal child develops the ability to pretend and understand pretence by the age of two, starts to use mental state terms by the age of three, and becomes capable of solving complex reasoning such as false belief tasks by the age of four [54,55]. However, a child has to learn to differentiate between what is real and what is pretend in order to build a consistent knowledge of the world [54,62]. In our model, the motor system subserves mental simulation and mental state inference by implicitly assuming the existence of a mechanism to *mark* the mental state representations as real or imagined. When in 'observer
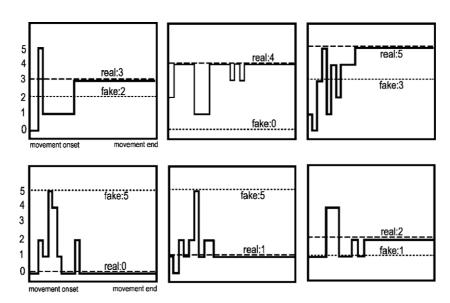

Fig. 8. A deceptive observer can infer the mental state of a deceptive actor. The number of target points used was six but only six representative deception scenarios are shown out of 6×5=30 possible. The conventions used are as in Fig. 7.

mode', the Estimated Mental State and Mental State are place holders for fictitious states, namely the intention and goals of the observed actor, which are decoupled from reality (they are neither observer's intention nor necessarily the object/affordance the actor means to act upon) and can be manipulated within the mental state inference mechanism. Our model provides an explicit mechanism as to how to utilize an existing forward model such that it can support a mental simulation system decoupled from the real world, which is fundamental to mental state inference [54].

Our model is compatible with the suggestion that mind reading is facilitated by imitative games and pretend play. We see a child's pretend play as an exercise to develop the ability to manipulate the contents of mental State (see Fig. 2) with proper tagging of *real* or *imagined*. 'If this banana was a telephone what would I do' is answered by modifying the representation of the (real) banana so that the affordances of a (virtual) phone is somehow (e.g. based on the shape) anchored on the banana. This allows the motor system to treat a banana as a phone using the anchored affordances to act on. Conversely, the child's understanding of the pretend play of others is an exercise in mental state inference where the search is over the possible modifications of the representation of the banana so to make the representation compatible with the observed action. In this sense, the mental state module (see Fig. 2) contains codes which are modifiable in part or all by the actor either for self-action (pretence—true act if not modified) or for understanding others' action. As a corollary, the imitation ability offered by the current model is based on reproducing the inferred intention of an observer which may not respect the details of the observed act. Imitation and its development is a vast topic and a full discussion is beyond the scope of this paper; the interested reader is referred to Ref. [89] and citations therein.

It takes a child 2 more years to move from the pretend play stage to adult like theory of mind that enables him/her to appreciate false belief tasks [54,55]. Our model predicts
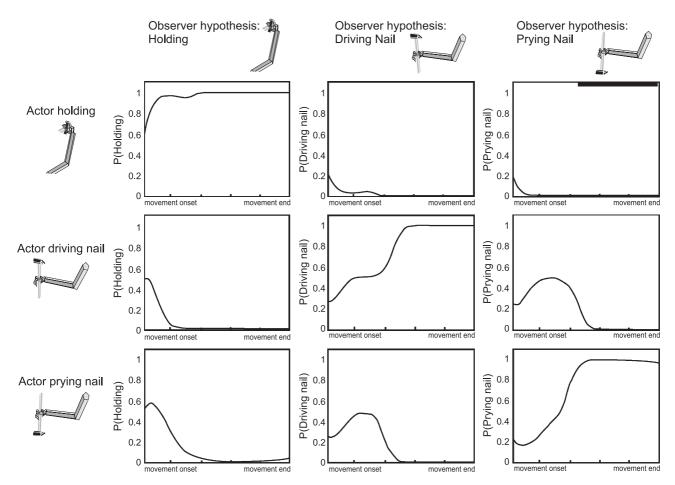

Fig. 9. The difference between visually extracted control variables and control variables obtained by mental simulation can be used to infer the intention of an actor. Each subplot shows the probability that the observed movement (rows) is the same as the mentally simulated one (columns). The horizontal axis represents the simulation cycles starting from movement onset to movement completion. The control variables extracted for the comparison is based on the mentally simulated movement. Thus, the first column inferences require the control parameters for holding (distance to metal head and the angle between the palm normal and hammer plane) whereas the remaining columns require the control parameters for nailing and prying (distance to handle center and the angle between the knuckle vector and hammer handle direction). The convergence to unity of the diagonal belief curves indicates correct mental state inference.

that this delay is due to the time required for the child's 'invention' of a (neural) representation of abstract mental states (believing vs. feeling hungry). Once it is acquired, the proficiency acquired by pretend play enables a child to instantiate representations of others' mental states (believe *something*) and perform the mental state inference loop (searching *something*) to find out why, for example, when going out, his/her mother (erroneously) picked her umbrella on a sunny day (because she believed it was raining).

4.3. Why mental state inference via mental simulation?

The ability to estimate the mental state of others could be acquired by learning the relation between one's own mental states and their visual consequences, and inverting the relation to infer mental states of others. However, the inversion is computationally hard due to the lack of a one-to-one correspondence between mental states and behavior. In fact, considering the unobservable parameters, the relation between mental states and behavior (in either direction) is not a well-defined function. Although one may suggest that primates have developed specialized dedicated neural circuits for dealing with such estimation tasks, we emphasize two points that favor a mental simulation mechanism over a dedicated circuit. First, mental state inference using mental simulation allows interpretation without prior experience since, as long as a movement or behavior is in the repertoire of an organism, it will be interpretable *without any training*. Second, a *fixed amount* of resource is required to implement the mental simulation circuit as opposed to a dedicated neural circuit that requires an ever-growing storage requirement with the increasing number of behaviors to interpret. These two features make mental simulation a parsimonious evolutionary solution for action understanding. On the other hand, for novel behaviors or actions performed by agents with different anatomical structures, the mental simulation strategy alone may not be enough. Thus, we suggest that mental simulation could be a strategy adopted by biological systems along the evolutionary scale, as it is cheap in terms of time and resource allocation. However, by the increasing complexity of environment and social life, other mechanisms might have augmented this 'cheap solution'.

A functional parallel to our model has been the findings on empathy and emotion understanding [8,88]. According to these studies, a common face-emotion region for both production and understanding appears to be the Insula [8,88]. Although it is tempting to accept this system as a 'emotional mirror neuron system', there is an important difference how these circuits could be learned (developed in infancy), assuming that these circuits are not innate. Hand actions provide self-vision directly; whereas facial gestures can only be observed via a reflective substance or otherwise must be inferred, e.g. from somatosensory perception (which itself has the problem of learning the

internal state→visual mapping). To match an observed action onto an internal motor representation a comparison must be performed, which requires the representations be in the same domain. Since an observer cannot infer either the somatosensory perception or the motor commands of the actor, there is a major computational problem for the brain, which requires a different solution than we have presented with our model.

If we disregard the unlikely hypothesis that the 'emotional mirror system' is innately wired, then the solution must be rooted in social interaction. "You eat A→you have face expression X (visual)". "I eat A→I feel disgust Y (internal state)". Therefore X (visual) must be Y (feeling of disgust). The mechanism of how this example could be elaborated in the brain is beyond the scope of this paper but the important message that should be taken is that the manual action understanding and facial emotion understanding pose rather different problems to the primate brain.

4.4. Biological considerations

Area F2 (caudal dorsal premotor cortex) in macaque monkey receives somatosensory input from areas PEip and PEc, and visual input from areas MIP and V6A, and projects to the primary motor cortex [32]. V6A reach-related neurons can be useful in guiding the hand to reach its target as the majority of V6A neurons tested in a reaching task were significantly modulated during the execution of arm movements [19]. Area F2 can use the MIP and V6A inputs in controlling arm position during the transport of the hand to spatial targets [68]. It is possible that the dorsal premotor cortex (areas F2 and F7) functions as a visuomotor controller that is involved in selection, preparation and execution of movements [91]. However, there are differences in F2 and F7 connectivity and neurophysiological responses, thus it is not clear whether they form separate circuits [32] or they are part of a unitary visuomotor circuit.

Similar to F2 and F7, area F4 (caudal ventral premotor cortex) receives rich input from posterior parietal cortex, the dominant projection being from area VIP, and sends descending projections to the brain stem and spinal cord [32]. In area F4, the space is coded in body-parts-centered coordinate frame (e.g. centered on the hand) [25], where many neurons fire during reaching movements of the proximal arm indicating that VIP–F4 circuit can be involved in reach control, transforming object locations into motor plans [68].

The neurons in area AIP (anterior part of the lateral bank of the intraparietal sulcus) discharge in response to viewing and/or grasping of three-dimensional objects representing properties of objects relevant for grasping [60,75,73]. AIP neurons are active either in relation to the grasping behavior alone or in relation to the vision of objects, and often a mixture of the two [74,85]. Area

AIP has very significant recurrent cortico-cortical projections with area F5 (rostral ventral premotor cortex) [56] that is involved in grasp planning and execution [69], and projects to motoneurons that control finger muscles [16]. However, F5 projections are not sufficient alone to perform a grasping action, as a lesion of the finger area in the primary motor cortex completely disrupts grasp execution whereas inactivation of F5 neurons only disrupts the coordination of fingers [24]. The latter finding suggests that area F5 'instructs' lower motor centers for execution and is not directly involved in controlling finger muscles supporting the structure of our model. In addition, it is suggested that the premotor cortex may play a preferential role in sensory or context-dependent processing related to task performance, whereas motor cortex may be more involved in processing related to the purely motor aspects of task performance [77].

The mental state inference model is based on a systems level abstraction of the briefly reviewed literature employing an object centered representation (in the simulations distance and orientation with respect to a target axis). Although this representation is compatible with the reports that parietal cortex employs object centered representation of the world-for-action, the exact form of the code and the subsequent transformations (e.g. normalization) are not known [1,90]. To summarize, the model assumes the following. For the control of goal-directed movement, parietal areas are involved in monitoring the relation of hand with respect to an attended object or a point in space. The premotor cortex, on the other hand, instructs the primary motor cortex and related structures for movement execution. The parietal and premotor cortices together with other lower centers form a visuomanual servo for a range of goal-directed movements, which are modulated by prefrontal cortex according to context and task requirements.

This hierarchical view might be questioned within the light of recent findings that employed long (500 ms) microstimulation of the monkey motor cortex [35]. In this study, the prolonged stimulation generated complex movements with repeatable robustness. The mapping of the movements onto the motor cortex suggested that the primary motor and premotor cortex might be complementary regions belonging to a larger map of manual space [35,36]. However, it should be noted that the prolonged microstimulation could be misleading and not conclusive due to the wide spread of applied current over the cortex [84]. In addition, we note that the movements generated in prolonged microstimulation study appear to be *feedforward* in nature and do not relate to an external goal. In contrast, our model attains the ability of mental state inference by utilizing a *feedback* control mechanism that is defined with respect to an external goal. Nevertheless, the direct and indirect projections of the premotor cortex onto the spinal cord [16,17] and the modulation of primary cortex neuron outputs by the premotor cortex [79] suggest that the strict hierarchical control view he have adopted could be simplistic and other alternatives [17,35,36,49] should be considered for future research.

It has been suggested that for imitation, a representation of a candidate movement is generated in the superior temporal sulcus (STS) as a forward prediction mediated by the mirror neurons and compared to the observed action representation in STS [8,41,58]. If this hypothesis is correct, then we might associate STS with the difference module, which generates an error signal between the mentally simulated and observed sensory signals (see Fig. 2). If this view is correct, then our model predicts that within STS a goal-directed movement is represented as a temporal profile of control parameters (e.g. grasping an object might be represented as the set trajectories of finger positions with respect to the object.) in a perspective- and actor-invariant way.

As the mental state inference model is a systems level model, it leaves certain issues open for future research. Firstly, the model's biological instantiation needs to be addressed, that is, how can the functional roles assigned to the modules within the model be realized using realistic neurons. An initial attempt would be to implement the postulated functions of the modules using population of neural units. This would then lead to neural level predictions that can be compared against neurophysiological data directly.

4.5. Mirror neurons and unconscious mental simulation

In one study, callosotomy patients could judge stimulus handedness accurately when the handedness of the stimulus is contralateral to the hemisphere perceiving it and was unable to judge it when the handedness of the stimulus was ipsilateral to the hemisphere perceiving it [67]. Response time analyses indicate patients, like controls, mentally simulate reaching ('molding') into stimulus postures [67]. The finding shows that mental simulation of a limb requires circuits specific to control of that limb in order to elicit correct response (i.e. recognition or inference), supporting our model that movement understanding requires the proper functioning of the motor circuit producing the movement.

The 'mirror neurons' in the ventral premotor cortex of a macaque monkey become active when the monkey observes goal-directed movements, suggesting that movement observation involves functioning of various cortical motor centers [15,29,70]. In addition, unconscious motor circuit involvement in movement observation is shown in humans using non-invasive techniques [6,18,38,42]. However, the functional role of such involvement is still unknown. Our model gives an answer by predicting that the activity in premotor areas is the result of unconscious or implicit *mental simulation* of movement analogous to the engagement of implicit motor imagery when subjects

are asked to report whether the presented stimulus is a left or right hand [65], or when they are asked to decide how they will grasp a handle with varying orientations [45]. During a mental simulation, the brain regions implementing the body and a sensory forward model (FM) should become active. Such a forward model could be implemented exclusively within the premotor cortex, in particular by the mirror neurons. According to this view, mirror neurons can be involved in the *sensory forward prediction* of goal-directed hand movements, which are activated for (1) mental simulation during action observation and (2) for feedback-delay compensation during movement. The experimental findings so far are in accordance with the FM account of mirror neurons: A muscimol-induced lesion in area F5 where mirror neurons were found does not impair grasping behavior but only cause a slowing down in movement execution [24] which supports the forward prediction for delay compensation role of mirror neurons. On the other hand, the mirror neuron discharge for action observation (see Refs. [29,70]) is compatible with an action understanding mechanism based on a mental simulation loop involving mirror neurons.

However, the hypothesis that mirror neurons implement a FM (or part of) is not the only alternative: it is possible to have a series of forward models implementing the functionality of the proposed FM. One possibility is to have a visual forward model located in the parietal cortex, mimicking the sensory processing from retina to parietal centers, which is connected in serial with a cerebellar dynamics forward model [51,92]. The latter alternative predicts that movement observation must activate cerebellum (limb dynamics forward model) and some region in the parietal cortex (sensory forward model) in addition to premotor regions (movement planning), which conforms well with the neuroimaging findings employing human subjects [6,43]. In the macaque, the primary reports of mirror neuron findings are confined to a sector of the inferior frontal cortex (area F5). Although some mirror-like neurons have been described in the anterior inferior parietal cortex (area 7b) [23], human 'mirror regions' appear to be more widely distributed than macaque mirror regions, including the parietal and premotor cortices [6]. However, there might be mirror areas in the macaque brain that have not been identified yet.

Current experimental findings do not help us rule out whether a circumscribed mirror region (i.e. in the premotor cortex) implements the proposed FM, or a series of forward models distributed over the cortex and the cerebellum make up a composite FM. Careful experiments must be designed with respect to the computational account of mental simulation theory of action understanding. A class of behavioral and brain imaging experiments can be designed using the following basic experimental setup. Subjects could be asked to infer the demonstrator's reach target [intention] as quick as possible, similar to our simulation experiments while simultaneously executing (or mentally imagining the execution of) reaching [grasping] movements. In such an experiment, our model would predict that the responses of the subjects would be faster and more accurate when the observer and the demonstrator's movements are characterized by compatible intentions, whereas it would be slower and less accurate with conflicting intentions. To reveal the mirror neuron involvement in mental simulation and mental state estimation, neurophysiological experiments must involve synchronized kinematics recordings of the experimenter (or monkey) during action demonstration. The correlation between the discharge profiles of mirror neurons with various visual feedback parameters for grasping, both when the monkey observes or executes a grasping movement, will reveal crucial information about the computational role of mirror neurons during manual control and action understanding, which can be used to verify/revise the model we presented in the paper.

The model we have developed presents a computational account of how mental state estimation could be built upon a visual feedback control mechanism. With the proposed localization of mental state estimation circuitry and the alternatives suggested for forward model localization, we believe that the model will lead to experimental studies that will not only improve and detail our modeling, but place our understanding of mirror neurons and mental state inference in a causally complete computational framework.

Appendix A

A.1. Straight-line reaching

Straight line reaching is achieved using the pseudo-inverse method. The method is based on the geometric Jacobian ($\mathbf{J}$), which is a time varying matrix relating end-effector Cartesian velocity to the angular velocities of the arm joints as follows [96]:

$$\begin{bmatrix} \dot{x} \\ \dot{y} \\ \dot{z} \end{bmatrix} = \mathbf{J} \begin{bmatrix} \dot{\theta}_1 \\ \dot{\theta}_2 \\ \dot{\theta}_3 \\ \dot{\theta}_4 \end{bmatrix} \quad \text{or in vector notation } \dot{p} = \mathbf{J}\dot{\theta}$$

Representing the upper arm length and the lower arm length as l_1 and l_2, respectively, and abbreviating $\sin(\theta_k)$ and $\cos(\theta_k)$ with s_k and c_k, where k is an index to the joint angle, the Jacobian matrix of our arm model can be written as:

$$\mathbf{J} = \begin{bmatrix} 0 & l_2(-c_2 s_4 + s_2 s_3 c_4) - l_1 c_2 & -l_2(c_2 c_3 c_4) & l_2(-s_2 c_4 + c_2 s_3 s_4) \\ l_2(-s_1 c_2 s_4 - (s_1 s_2 s_3 c_4 + c_1 c_3 c_4)) + l_1 s_1 c_2 & l_2(c_1 s_2 s_4 + c_2 s_3 c_1 c_4) + l_1 c_1 c_2 & l_2(c_1 s_2 c_3 c_4 + s_1 s_3 c_4) & -l_2(-c_1 c_2 c_4 - c_1 s_2 s_3 s_4 + s_1 c_3 s_4) \\ l_2(-c_1 c_2 s_4 + c_1 c_4 s_2 s_3 - c_3 c_4 s_1) - l_1 c_1 c_2 & l_2(-s_1 s_2 s_4 + c_2 c_4 s_1 s_3) + l_1 s_1 s_2 & l_2(-c_3 c_4 s_1 s_2 - c_1 c_4 s_3) & l_2(-s_1 c_2 c_4 - s_1 s_2 s_3 s_4 - c_1 c_3 s_4) - l_1 c_1 c_2 \end{bmatrix}$$

A desired end-effector position p_{desired} can be achieved by iterating the below update rule until $p \cong p_{\text{desired}}$, where η represents the update rate and $\mathbf{J}^{\#}$ is the pseudo-inverse of $\mathbf{J}$. We adapted η as a function of end-effector–target distance (d) as $\eta = 0.5 + e^{-0.02d}$ to obtain faster convergence. Note that the visual feedback signal appearing in this computation is $p_{\text{desired}} - p$.

$$\theta_{t+1} = \theta_t + \eta \mathbf{J}^{\#}_{\theta_t}(p_{\text{desired}} - p_t)$$

A.2. Deceptive reaching

Deceptive reaching is characterized by a real (p_{real}) and a fake (p_{fake}) target. We denote the end-effector position by p. A 'floating target' for the inverse kinematics can be used to generate a deceptive trajectory. The desired target moves from the fake target to the real one. The function f is an increasing function between 0 and 1 in the domain of v, where v denotes the distance between the board plane and end-effector (v_0 denotes the distance at the movement onset.)

$$p_{\text{desired}}(v) = f(v)p_{\text{real}} + (1 - f(v))p_{\text{fake}}$$

In the simulations, we used $f(v) = 1 - \sqrt{v/v_0}$ and ran the inverse kinematics algorithm (straight line reaching) with the time varying target p_{desired}. The visual feedback signal appearing in the inverse kinematics computation can be expanded as follows:

$$p_{\text{desired}}(v) - p = f(v)(p_{\text{real}} - p) + (1 - f(v))(p_{\text{fake}} - p)$$

Thus, the control variables extracted by parietal cortex are taken as the distances from the end-effector to the fake and real targets, hence this two distance values guided mental state search.

A.3. Spiral reaching

Spiral reaching movements are generated by applying a visual feedback servo for a 'floating target' based on a set of via-points (constructed in an object centered manner), weighted according to the distance of the hand to the board. Desired end-effector position is given below using the following variables:

v: distance between the board plane and the end-effector (p)
v_0: value of v at movement onset
c: board center

$$p_{\text{desired}}(v) = c + \sum_{k=0}^{8} \frac{e^{\left(\sqrt{1-v/v_0} - i/8\right)^2 / 0.01}}{\sum_{m=0}^{8} e^{\left(\sqrt{1-v/v_0} - m/8\right)^2 / 0.01}} \begin{bmatrix} \cos(\pi + k\pi/8) & -\sin(\pi + k\pi/8) & 0 \\ \sin(\pi + k\pi/8) & \cos(\pi + k\pi/8) & 0 \\ 0 & 0 & 1 \end{bmatrix} (p_{\text{target}} - c)$$

The movement kinematics was generated as in straight line reaching using the p_{desired} as the target. The online feedback control of this movement requires monitoring of eight virtual targets (this is evident via an expansion similar to the one in deceptive reaching). Thus, end-effector–virtual target distances (i.e. the terms of the summation in the above equation) are used as control variables in the mental state inference.

A.4. Hammer-grasp for nailing and prying

Grasping of a hammer suitable for prying or driving a nail is modeled as a power grasp of the handle. The difference between nailing and prying movements is characterized by the orientation of the hand in relation to the hammer. We modeled the grasp as two parallel visual feedback control problems: (1) transporting the hand to the proximity of the center of the handle and (2) orienting the knuckle vector to match the orientation of the handle (either fully aligned or π radians away). The reaching component of the grasping movement is solved using the inverse kinematics algorithm introduced earlier. The
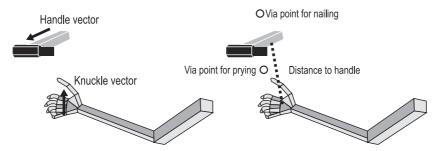
Fig. 10. The control variables used in nailing and prying tasks are depicted. The desired Knuckle vector is −(Handle vector) for prying and (Handle vector) for nailing. The desired Distance for both cases is zero. The path of the hand is constrained with appropriate via-points to avoid collision.

orientation of the hand is adjusted by stochastic gradient descent based on feedback of the orientation error. Thus the control variables that enable the generation of grasping movement were (1) the orientation difference (angle) between the knuckle vector and hammer handle and (2) the distance of the hand to the handle center. The mental state search was therefore based on the distance and orientation variables (see Fig. 10).

The algorithm used for simulating grasping kinematics performs various tasks starting from the onset of movement (time: 0) until the completion of a grasp (time: 1):

0.00–1.00: Reach towards the handle center via a via-point (to avoid collision)
0.00–0.70: Extend fingers
0.30–0.95: Adapt hand orientation
0.95–1.00: Check for collision
　　If collision: Enclose fingers.

Note that the fingers play a rather decorative role in this simulation, as they are not part of feedback control in power grasping.

A.5. Hammer-grasp for holding/putting away

Grasping of a hammer with no intention of tool-use is modeled as power grasping the metal head. We model the grasping as two parallel visual feedback control problems: (1) transporting hand to the proximity of the center of the metal head and (2) adapting the hand orientation such that palm normal coincides with the hammer plane normal (see Fig. 11).

The reaching component of the grasping movement is solved using the inverse kinematics algorithm introduced earlier. The orientation of the hand is adjusted by stochastic gradient descent based on the mismatch between palm and hammer plane normal vectors. Thus, the control variables that enabled the generation of grasping movement were (1) the orientation difference (angle) between the palm normal and hammer plane normal and (2) the distance of the hand to the metal head center. The mental state search was, therefore, based on the distance and normal differences described. The algorithm used for simulating grasping kinematics is the same as nailing and prying movement generation presented above.

Note that the orientation and distance not only comprise a minimal set of parameters that can be used to generate movements for grasping a hammer, but also allows mental state inference without explicit coordinate transformation. Although the grasp-planning algorithm we implemented is a general framework that can operate for simple scenarios, certain hammer orientations/locations would require more advanced planning and control schemes (e.g. better collisions avoidance). Nevertheless, the current simulations give us a simple framework to demonstrate how the goal-directed movement control variables could be used to infer another actor's intention.
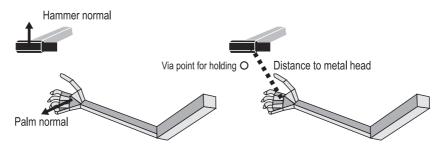

Fig. 11. The control variables used in holding task is depicted. Desired palm normal is hammer plane normal. The desired distance is zero. However, the path of the hand is constrained with a via-point avoiding collision.

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