

Interplay Between Conceptual Expectations and Movement Predictions Underlies Action Understanding

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Recent accounts of understanding goal-directed action underline the importance of a hierarchical predictive architecture. However, the neural implementation of such an architecture remains elusive. In the present study, we used functional neuroimaging to quantify brain activity associated with predicting physical movements, as they were modulated by conceptual-expectations regarding the purpose of the object involved in the action. Participants observed object-related actions preceded by a cue that generated both conceptual goal expectations and movement goal predictions. In 2 tasks, observers judged whether conceptual or movement goals matched or mismatched the cue. At the conceptual level, expected goals specifically recruited the posterior cingulate cortex, irrespectively of the task and the perceived movement goal. At the movement level, neural activation of the parieto-frontal circuit, including inferior frontal gyrus and the inferior parietal lobe, reflected unpredicted movement goals. Crucially, this movement prediction error was only present when the purpose of the involved object was expected. These findings provide neural evidence that prior conceptual expectations influence processing of physical movement goals and thereby support the hierarchical predictive account of action processing.

Keywords: action hierarchy, action perception, active inference, anticipation, predictive coding

Introduction

The ability to predict other individuals' behavioral goals is a crucial prerequisite for success in human society (Tomasello 1999). In order to attain desired goals, humans recruit behavioral policies that guide effective use and manipulation of objects (Roy and Square 1985; Ochipa et al. 1992; Hodges et al. 2000; Johnson-Frey 2003; Martin 2007). Control of object-related behavior relies upon previously acquired conceptual knowledge regarding functional relationships between objects in the world (related to their purpose) and the knowledge of relationships between objects and the body that guides movement (Roy and Square 1985; Johnson-Frey 2003; Pearson et al. 2011; Friston et al. 2012). In the present study, we aimed to investigate how general conceptual-expectations about the purpose of the used object and movement predictions regarding the actor's movement goal location contribute to understanding of observed object-related behavior (De Lange et al. 2008; Adolphs 2009; Koster-Hale and Saxe 2013).

At present, the neural mechanisms that underpin the ability to make sense of others' observed goal-directed behavior remain in dispute (Jacob and Jeannerod 2005; Csibra 2008; Bekkering et al. 2009; Ferrari et al. 2009; Hickok 2009; Hauser

and Wood 2010; Rizzolatti and Sinigaglia 2010). The perceptuo-motor account explains action understanding as mapping of the observed movements to observers' "action observation/mirroring network (AON)," which is also involved in movement production (Gallese and Goldman 1998; Flanagan and Johansson 2003; Rizzolatti and Craighero 2004; Ferrari et al. 2009; Rizzolatti and Sinigaglia 2010). On the other hand, the "mentalizing/theory of mind" accounts propose that understanding other individuals' actions relies on the inference of their hidden mental states, such as beliefs and desires, which consistently activates a "mentalizing network" (Fletcher et al. 1995; Saxe and Kanwisher 2003; Frith and Frith 2006; Brass et al. 2007). Recent neuroimaging findings suggest that the "mirroring/AON" and "mentalizing" cortical systems play complementary roles during action understanding (Brass et al. 2007; De Lange et al. 2008; Spunt and Lieberman 2012).

Theoretical models are beginning to stress the important role of hierarchical predictive signaling during cognition in general (Bar 2009a, 2009b; Friston 2010) and action understanding in particular (e.g., Clark 2013; Kilner et al. 2007; Friston 2011; Friston et al. 2011; Koster-Hale and Saxe 2013), which offers the possibility to unify perceptuo-motor and mentalizing theories. The active inference account (Friston et al. 2011, 2012), derived from the free-energy principle (Friston 2010), asserts that a hierarchy of predictions, which is used for attainment of observers' own behavioral goals, also facilitates the ability to infer goals of other individuals. Here, we distinguish between conceptual goal expectations regarding the purpose of observed objects (e.g., a rose, perfume, or French cheese can be used for smelling) and more concrete movement goal predictions pertaining to moving an object into a new position (e.g., smelling typically goes with movement to the nose, Kilner et al. 2007; Friston et al. 2011). The predictive mechanism in the parieto-frontal "mirroring/AON" circuit, which include parts of the inferior parietal lobule (IPL) and the inferior frontal gyrus (IFG) is suggested to play an important role in processing other individuals' goal-directed movements (Umiltà et al. 2001; Fogassi et al. 2005; Newman-Norlund et al. 2007; Press et al. 2012). However, the role of conceptual-expectations in identifying the purpose of observed object-directed movements remains elusive. More generally, there is a lack of evidence for a hierarchical mechanism, in which both conceptual-expectations about the overall purpose of the object in the world and predictions about specific bodily movements underlie understanding of another individual's actions.

Here, we tested the claim that the processing of a movement goal depends on the expectation regarding the observed individual's conceptual goal when using a specific object (Friston

et al. 2012; Ondobaka and Bekkering 2013). We hypothesized that during processing of movement goals, activity in the parieto-frontal circuit depends on the concurrently expected conceptual goal related to the purpose of the object that is involved in the action (e.g., a rose is for smelling). To examine the neural signatures of the hierarchy of conceptual and movement anticipation, we combined functional magnetic resonance imaging (fMRI) with an action anticipation paradigm. In 2 tasks, participants judged the same object-related actions by focusing either on the conceptual goal (i.e., choice of a purposeful object) or on the movement goal (i.e., the end location of the movement). We show that action processing entails a multi-tiered mechanism, in which conceptual-expectations regarding the purpose of a particular object influence perceptual predictions that are involved in processing of the observed object-related movements.

Materials and Methods

Participants

The study was approved by the local ethics committee and in accordance with the Helsinki declaration. Participants were 15 (4 males) right-handed, proficient Dutch speakers with no history of neurological illness and no contraindications to fMRI scanning (mean age: 24.7 years; range: 21–29 years). Data from one participant were discarded due to technical problems with the response apparatus. Participants were recruited from the online Research Participation System of the Radboud University Nijmegen and received either 10 euro/h or course credits for their participation. All participants gave informed consent prior to taking part.

Behavioral Procedure and Analysis

On each trial, participants observed a word-cue (e.g., “to smell”), followed by a picture in which an actor had transported a particular object to a particular location (e.g., a rose moved to the nose; see Fig. 1 and Table 1). We ensured that the cue simultaneously related to both the conceptual goal (i.e., choice of a functionally purposeful object) and the movement goal (i.e., specific movement goal required). We reasoned that the inference of a conceptual goal should depend on the general expectation about the objects’ properties, since different objects could be used to attain the same goal (e.g., smell goes with roses or perfume, but not headphones, see Roy and Square 1985). In contrast, inference of a movement goal should be independent of the object’s purpose because a specific movement goal can always be predicted (e.g., smell goes with movement to the nose, not to the ear, see Roy and Square 1985). This resulted in a design in which the observed action was either expected or unexpected with respect to the primed conceptual goal, and predicted or unpredicted in terms of its movement goal.

Each trial started with a presentation of one of 4 possible cues: “to taste,” “to listen,” “to smell,” “to look” for 0.5 s (Fig. 1). The cue was followed by a picture, presented for 2 s, which depicted an actor who had moved one of 12 possible objects to one of the 4 movement goal locations (i.e., mouth, ear, nose, gaze field). In order to avoid repetition of stimulus presentation, every picture was taken from 3 different angles: full frontal, 45° left and 45° right. The cue raised parallel expectations regarding the actor’s conceptual goal to use the object and perceptuo-motor predictions of the movement. Thus, the picture was either expected or unexpected with respect to the primed conceptual goal and predicted or unpredicted regarding the primed movement goal. In 2 separate blocks, participants were asked to complete a Conceptual task and a Movement task. The order of the 2 blocks was randomized among subjects, such that half of the subjects started with the conceptual task and the other half with the movement task. The instruction for the Conceptual task was “For the following word-picture pairs, judge whether the object matches the behavioral policy indicated by the word.” The instruction for the Movement task was “For the

following word-picture pairs, judge whether the end-goal of the movement matches the behavioral policy indicated by the word.” Participants responded by pressing one of 2 buttons with their index or middle finger of their right hand. The aim of the tasks was to determine whether the depicted actions were logical in terms of the conceptual goal (i.e., the actor’s choice to use a purposeful object) or the movement goal (i.e., the end location of the actor’s movement).

During the scanning phase, each task consisted of 144 trials (36 for each condition) and 11 “null events,” in which only a fixation cross appeared in the center of the screen. To optimize estimation of fMRI signal, trials were presented in a pseudorandom order with a random interval (2.5–4.5 s) before the onsets of both the cue and the picture, during which a fixation cross appeared. The stimulus-onset asynchrony (SOA) ranged from 8 to 12 s, leading to duration of ~25 min per task. Prior to scanning, participants were familiarized with all the objects, which were present in the scanner control room, and they practiced 48 trials per task to become familiar with the procedure. Stimulus presentation was controlled using Presentation software (Neurobehavioral Systems, Albany, NY). Reaction times (RTs) and Accuracy scores (ASs; percentage of correct responses) were recorded for subsequent behavioral analysis.

To assess participants’ task performance, we computed their Efficacy scores (Efficacy = ASs/RTs), a measure that combines the 2 common indices of behavioral performance. Because both RTs and ASs reflect performance (Pachella 1974; Ratcliff and Hacker 1981), a combined index of RTs and ASs was used as a performance measure (Woltz and Was 2006; Jo Nixon et al. 2007). This measure offers a useful solution for possible methodological issues that could arise due to possible differences in speed-accuracy criteria adopted by the participants in different experimental conditions (Pachella 1974).

Imaging Procedure and Analysis

MRI measurements were performed on a Siemens Magnetom Trio scanner. We acquired 29 slices (3 mm slice thickness, $3.5 \times 3.5 \times 3.0$ mm voxel size) in an ascending order using a multiple-shot echoplanar imaging sequence (time to repeat [TR]: 2230 ms; echo times [TE]: 9.4, 21.2, 33, 45, 56 ms; flip angle: 90°; field of view: 224 mm). Additionally for each participant, an anatomical image was acquired with a T_1 -weighted MP-RAGE sequence, using a GRAPPA acceleration factor of 2 (TR: 2300; TE: 3.03 ms; voxel size: $1 \times 1 \times 1$ mm).

We used SPM 8 (<http://www.fil.ion.ucl.ac.uk/spm>, Wellcome Trust Centre for Neuroimaging, London, UK) for image preprocessing and a whole-brain analysis. The first 5 volumes of the sessions were discarded to allow for T_1 equilibration. Functional images acquired at different echo times were first spatially realigned to the first image of the run and then combined together to a single set of images. Subsequently, all slices were temporally corrected to the first slice of each volume. Next, the structural image was coregistered to the functional images, and both structural and functional images were spatially normalized to the Montreal Neurological Institute (MNI) template. Finally, spatial smoothing of the functional images was performed with an isotropic Gaussian kernel with a full-width at half-maximum of 8 mm.

We used a standard two-level approach to perform the statistical analysis. At the first level, for each participant, we used an event-related general linear model to estimate the fMRI signal. Onsets of every picture were modeled with a Dirac delta function for each of the 8 conditions (2 Tasks \times 2 Conceptual-expectation \times 2 Movement-prediction). Also, the model included 8 regressors for the 4 different cue types and errors for each of the tasks, and regressors for instructions modeled with a delta function. Finally, the break between the 2 tasks was modeled as a boxcar of which the onset corresponded to the beginning of the break and the duration corresponded with its length. All regressors were convolved with the hemodynamic response function. Additionally, we modeled participants’ specific movement parameters and their first and second derivatives, adding up to 18 nuisance regressors. Linear contrasts of regression coefficients computed at the first level were taken to the second-level random-effects analysis, where we performed simple t tests for each of the contrasts of interest. The examined contrasts include the Main effect of Conceptual-expectation and Main Effect of Movement-prediction,

Conceptual task: Does the conceptual goal match the cue?
Movement task: Does the movement goal match the cue?



Figure 1. Stimuli and design. In both tasks, participants observed word-cues, which were followed by a picture of an object-related action. In the Movement task, they had to judge whether the perceived movement goal (e.g., an object that is moved to the nose) matched the cue (e.g., “to smell”). In the Conceptual task, participants observed the same stimuli, while they judged whether the expected conceptual goal (to purposefully use an object, for example, use a rose for smelling) matched the cue. See also Table 1 for the complete list of used stimulus material.

Table 1

Stimulus material

Primed behavioral policy	Congruent conceptual goal	Incongruent conceptual goal	Congruent movement goal	Incongruent movement goal
To look	Use stop-watch	Use French cheese	Gaze field	Nose
To look	Use book	Use apple	Gaze field	Mouth
To look	Use framed photo	Use transistor radio	Gaze field	Ear
To listen	Use ear phones	Use rose	Ear	Nose
To listen	Use seashell	Use cup	Ear	Mouth
To listen	Use transistor radio	Use framed photo	Ear	Gaze field
To smell	Use eau de toilette	Use sport bottle	Nose	Mouth
To smell	Use French cheese	Use stop-watch	Nose	Gaze field
To smell	Use rose	Use ear phones	Nose	Ear
To taste	Use apple	Use book	Mouth	Gaze field
To taste	Use cup	Use seashell	Mouth	Ear
To taste	Use sport bottle	Use eau de toilette	Mouth	Nose

Note: Table shows a description of conceptual-expectation and movement-prediction for the behavioral prime words and the action pictures that were used in the experiment.

Task × Conceptual-expectation interaction, Task × Movement-prediction interaction and Task × Conceptual-expectation × Movement-prediction 3-way interaction. The only significant Task × Movement-prediction interaction was followed by the examination of the underlying simple effects. To control for false positives over all tests, we applied family-wise error rate (FWE) correction for multiple comparisons with a cluster threshold of $P < 0.05$, on the basis of voxel-wise threshold of $P < 0.001$.

Results

Behavioral Results: Efficiency in Processing Observed Goal-Directed Behavior

To assess participants’ behavioral performance during judgment of others’ observed actions, we calculated their efficiency scores, a measure of performance that combines accuracy and response times (see Materials and Methods). Participants’ performance efficiency did not differ between the Movement task and the Conceptual task, $F_{1,13} = 0.01$, $P = 0.918$, $\eta^2 = 0.001$ (Fig. 2). Overall, participants were more efficient to judge

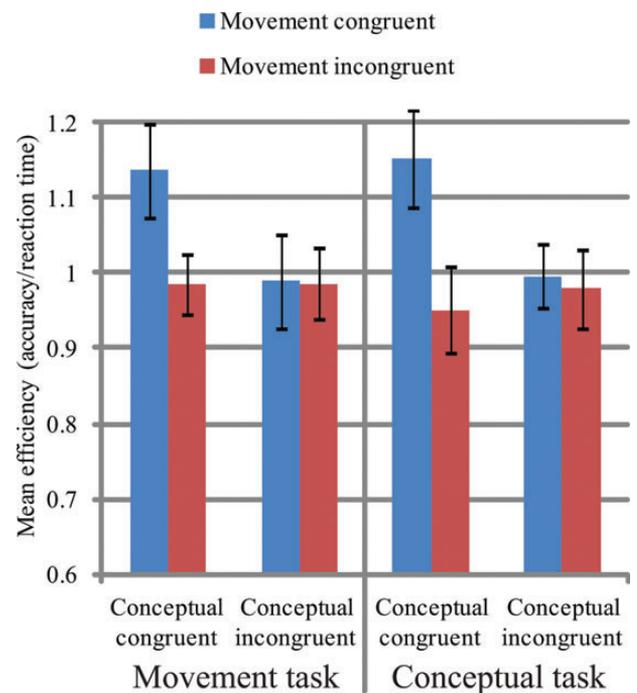


Figure 2. Behavioral performance. Participants’ mean efficiency scores in the Movement task and Conceptual task as a function of Conceptual-expectation and Movement-prediction. Error bars represent mean ± standard errors of the mean (SEM).

conceptual goals that were expected given the cue, $F_{1,13} = 13.01$, $P = 0.003$, $\eta^2 = 0.50$, compared with the unexpected ones. Similarly, they were more efficient to judge movement goals that were predicted given the cue, $F_{1,13} = 14.11$, $P = 0.002$, $\eta^2 = 0.52$, compared with the unpredicted ones.

We observed a significant interaction effect between Conceptual-expectation and Movement-prediction, $F_{1,13} = 54.19$, $P < 0.001$, $\eta^2 = 0.81$ (Fig. 2), suggesting that processing of movement goals is contingent on the conceptual goal expectation. Only when the conceptual goal was expected given the cue, were participants more efficient to judge predicted versus unpredicted movement goals, $t_{(1,13)} = 8.37$, $P < 0.001$. In contrast, when the conceptual goal was unexpected, the movement efficiency scores did not differ significantly, $t_{(1,13)} = 1.38$,

$P=0.19$. Moreover, the task did not influence performance efficiency during judgment of object-related behavior (Task \times Conceptual-expectation, $F_{1,13}=0.12$, $P=0.736$, $\eta^2=0.01$; Task \times Movement-prediction, $F_{1,13}=0.10$, $P=0.757$, $\eta^2=0.01$).

fMRI Results: Main Effects of Conceptual-Expectation and Movement-Prediction

The posterior cingulate cortex (PCC), a midline node of the “mentalizing network,” showed larger activity for expected than unexpected conceptual goals, given the primed behavioral policy ($P_{\text{corr}}=0.01$ for the Main effect of Conceptual-expectation, Fig. 3a and Table 2). Contrasting unexpected with expected conceptual goals revealed no significant differences in neural activity, even at a very liberal statistical threshold ($P_{\text{uncorr}}=0.05$). The activity in the PCC was, however, not sensitive to the perceptual information regarding the predicted movement goal, suggesting its specific involvement in processing of conceptual goals related to the purpose of the used

object. We ran an additional analysis which included an RTs regressor to exclude the possibility that the observed activity in the PCC was purely due to differences in reaction times between the 2 conditions. The results again showed a larger activity for expected than unexpected conceptual goals ($P_{\text{corr}}=0.002$) in the same PCC cluster, indicating that it is unlikely that the RT differences contributed to the observed neural effects. Comparing Movement-unpredicted and Movement-predicted condition revealed a significant cluster in the precuneus ($P_{\text{corr}}=0.03$ for the Main effect of Movement-prediction), whereas the inversed contrast did not reveal any brain regions that were more active in the Movement-predicted condition ($P_{\text{uncorr}}=0.05$).

fMRI Results: Interactions of Task with Conceptual-Expectation and Movement-Prediction

The lack of a significant interaction between Conceptual-expectation and Task ($P_{\text{uncorr}}>0.05$) suggested that conceptual

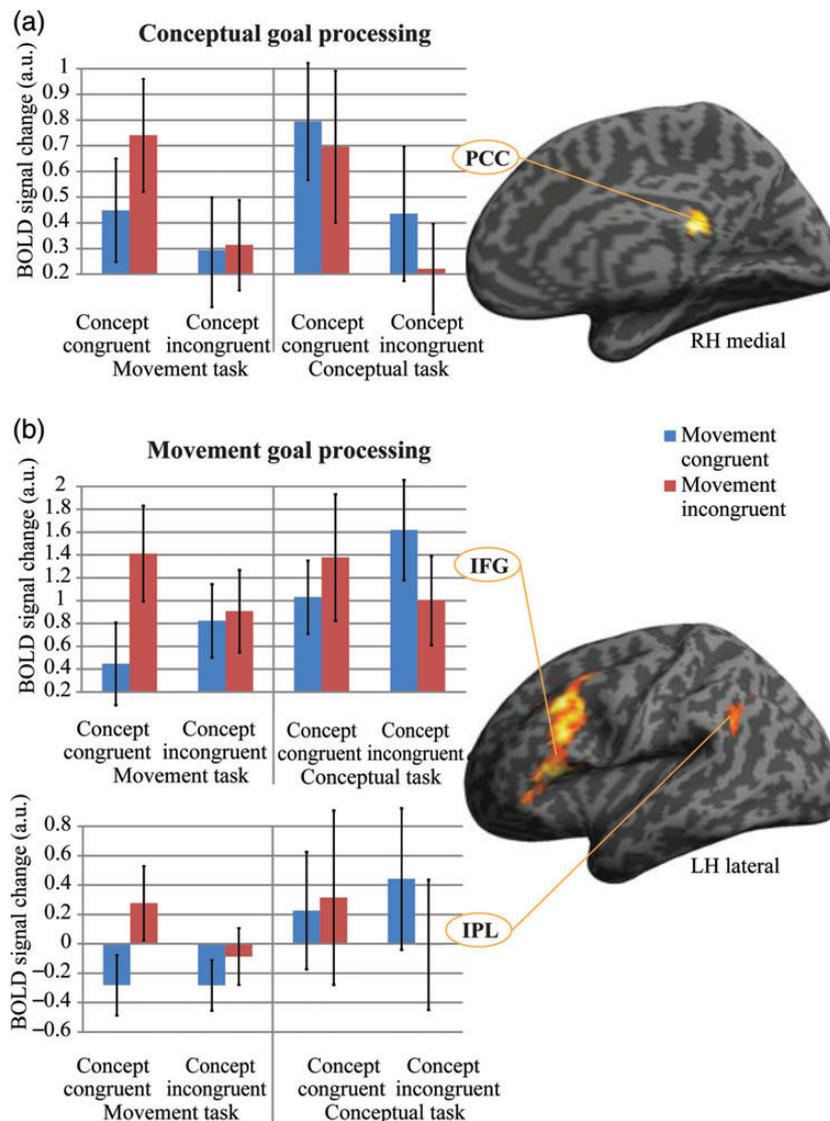


Figure 3. Neural processing of conceptual goals and movement goals. (a) Conceptual goals that were expected given the cue-evoked greater activity than the unexpected ones bilaterally in the posterior cingulate cortex (PCC). Conceptual processing in the PCC was independent of the task and of movement-prediction (signal change plot). (b) Left lateralized parieto-frontal network, including IFG and IPL, was sensitive to the processing of unpredicted movement goals in the movement task only and solely when the conceptual goal was expected (signal change plots). Bars represent mean \pm SEM. For exact localization of neural activations, see Table 2.

Table 2

Localization of neural activations

Contrast	Anatomical label	Peak coordinates (MNI)	Cluster size (nr. voxels)	Peak <i>t</i> -value	Cluster <i>P</i> -value (FWE-corrected)
Overall (movement task and conceptual task): Conceptual congruent > Conceptual incongruent					
	Posterior cingulate cortex	6 –38 18 –10 –34 22	182	7.89 6.05 5.47	0.012
Movement task: Movement incongruent/Conceptual congruent > Movement congruent/Conceptual congruent					
	Inferior frontal gyrus/middle frontal gyrus	–44 14 18 –52 18 6 –36 16 32	1708	9.03 8.31 7.90	0.001
	Inferior parietal lobe	–40 –50 30	130	6.16	0.033

Note: Spatial coordinates (*x*, *y*, *z*) of the cluster-peaks showing significant activations for conceptual and movement processing of observed goal-directed behavior. All significant clusters at $P < 0.05$ FWE-correction threshold are shown.

goal processing during action observation occurred independently of task focus (Fig. 3*a*). However, task did influence processing of movement goals. The parieto-frontal “action observation network (AON)” showed stronger activation for observed actions that mismatched the predicted movement goal compared with actions that matched the predicted movement goal in the Movement task, but not in the Conceptual task ($P_{\text{corr}} < 0.001$ for the whole-brain Task \times Movement-prediction interaction). We did not observe a three-way Task \times Conceptual-expectation \times Movement-prediction interaction ($P_{\text{uncorr}} > 0.05$).

fMRI Results: Prediction of Others’ Movement Goals in the Parieto-frontal Network

We focused our further analysis on the Movement task, in which the processing of unpredicted movement goals compared with predicted ones depended on the expectation regarding the conceptual goal to use a purposeful object ($P_{\text{corr}} = 0.001$ for the whole-brain Conceptual-expectation \times Movement-prediction interaction in the Movement task). Figure 3*b* shows the neural activation that resulted from the simple effect contrast Movement-unpredicted > Movement-predicted in the Conceptual-expected condition. This activation reflected the movement goal prediction error only when the conceptual goal matched the anticipated behavior. When conceptual goal mismatched the anticipated behavior, no movement goal prediction error related activity was apparent ($P_{\text{uncorr}} > 0.05$).

Discussion

The experiment reported here yielded 2 important findings. First, we found support for the contribution of the PCC in the processing of expected conceptual goals that are related to the purpose of an action. Second, the enhanced activation for unpredicted physical movement goals compared with the predicted ones in the parieto-frontal circuit indicates that it codes for movement goal prediction errors (Kilner et al. 2007; Friston et al. 2011; Press et al. 2012). Importantly, neural activity related to prediction errors that was associated with deliberate processing of movement goals was apparent only when the object used matched the corresponding conceptual goal. Together, these findings outline the brain networks involved

in the interplay between expectations and predictions that subserve the active inference of other individuals’ object-related behavior (Clark 2013; Wolpert et al. 2003; Kilner et al. 2007; Ondobaka and Bekkering 2013).

Contribution of Posterior Cingulate Cortex to Conceptual Inference of Action

Previous investigations on how observers infer other individuals’ internal models of the world that govern overt behavior have repeatedly reported activity in the midline structures, like the PCC (Fletcher et al. 1995; Saxe and Kanwisher 2003; De Lange et al. 2008; Spunt and Lieberman 2012). However, this region’s role in action understanding remains largely unclear. Here, we showed a specific contribution of the PCC to active inference of other individuals’ conceptual goals related to the choice of a purposeful object in the world—a process crucial for understanding object-related behavior (Johnson-Frey 2003; Hayden et al. 2008; Friston et al. 2012; Spunt and Lieberman 2012). The PCC was sensitive to expected conceptual goals pertaining to the purpose of the used object (e.g., utilizing a suitable object for smelling—a rose), but not to the physical movement goals (e.g., moving an object to the nose). This finding highlights the importance of the midline structures, including the PCC, in representing the organism’s conceptual model of the world that supports efficient processing of incoming sensory information (Clark 2013; Bar and Aminoff 2003; Raichle and Gusnard 2005; Bar 2009a, 2009b; Friston 2010). Behaviorally, the interactive processing of conceptual and movement goals is consistent with the fMRI results, suggesting that conceptual-expectations critically modulate the processing of immediate perceptuo-motor information from the environment (Raichle and Gusnard 2005; Bar et al. 2007; Kilner et al. 2007; Kveraga et al. 2011; Ondobaka et al. 2012; Wang and Hamilton 2012).

The observed pattern of neural responses in the PCC is in line with a recent proposal, derived from macaque neurophysiology (Hayden et al. 2008; Pearson et al. 2009), which suggests that this region controls the deployment of behavioral policies and learning of new ones for successful guidance of future behavior (Pearson et al. 2011). Our results extend this claim and suggest that the PCC also supports processing of another individual’s behavioral policies that govern their overt object-related behavior (Wolpert et al. 2003; Friston et al. 2011). Moreover, the finding is in agreement with the suggestion that midline cortical structures, including the PCC, generate conceptual-expectations about the upcoming future events in the outside world that are necessary for understanding the purpose behind others’ observed behavior (Buckner and Carroll 2007).

Contribution of Parieto-Frontal “Action Observation Network” to Action Inference

One of the heavily debated topics in cognitive neuroscience regards the role of observer’s perceptuo-motor circuits, which are recruited to attain their own movement goals, in the general understanding of others’ goal-directed behavior (Gallese and Goldman 1998; Jacob and Jeannerod 2005; Csibra 2008; Ferrari et al. 2009; Hickok 2009; Rizzolatti and Sinigaglia 2010; Kilner 2011). Here, we show that the parieto-frontal circuit including anterior IFG and posterior IPL—regions that are canonical parts of the “action observation network”—encode the

perceived physical movement goal (Johnson-Frey et al. 2003; Fogassi et al. 2005; Press et al. 2012). More abstract movement goals are directed toward a particular location in the environment (Johnson-Frey et al. 2003; Fogassi et al. 2005; Shima et al. 2006; Newman-Norlund et al. 2007; Bonini et al. 2011) and should be distinguished from the more concrete motor goals, reflected in the posterior IFG/premotor cortex and anterior IPL, that relate to manipulating of a particular object (Rizzolatti et al. 1996; Hamilton and Grafton 2007; Kilner et al. 2009; Kilner 2011; Spunt and Lieberman 2013). The observed parieto-frontal circuit activation reflected the movement goal prediction error that is generated in the observer's perceptuo-motor system, but only when the observers' task was to judge whether the movement goal matched their sensory prediction. The parieto-frontal circuit was, however, not directly sensitive to the conceptual goal to utilize a particular object that matches the purpose. These results are in line with previous findings that show a crucial contribution of the "action observation network" to the processing of movement goals (Pobric and Hamilton 2006; Newman-Norlund et al. 2007; De Lange et al. 2008; Spunt et al. 2010; Press et al. 2012) in situations where no general conceptual-expectations were generated prior to action observation.

Expectations and Predictions in Processing Another Individual's Goal-Directed Behavior

Our data show that the "movement goal" prediction error, coded in the parieto-frontal circuit, depends on the general expectation about the purpose of the object that is involved in the action. These results are in line with recent theoretical accounts of action understanding that stress the importance of combining perceptual information about goal-directed movements with the observer's conceptual world knowledge. (De Lange et al. 2008; Adolphs 2009; Teufel et al. 2010; Spunt and Lieberman 2012; Wang and Hamilton 2012). Whereas perceptuo-motor experiments have emphasized the role of the parieto-frontal circuit in processing others' movement goals (Gallese et al. 1996; Buccino et al. 2001; Bosbach et al. 2005; Hamilton and Grafton 2008), conceptual theories of action understanding have proposed that mentalizing about others' conceptual goals is fundamental to understanding others' behavior (Jacob and Jeannerod 2005; Saxe 2006; Csibra 2008; Hauser and Wood 2010). The current findings provide evidence for the involvement of a multitiered anticipatory mechanism in the processing of conceptual and perceptuo-motor aspects of object-related behavior (Clark 2013; Kilner et al. 2007; Friston et al. 2011). Hierarchical predictive coding offers a new framework in which action understanding is based on prior expectations regarding both the purpose of the used object and the prediction about the physical movement goals. Crucially, this framework allows a synthesis of perceptuo-motor (Gallese and Goldman 1998; Rizzolatti and Sinigaglia 2010) and conceptual theories (Frith and Frith 1999, 2006) of social cognition.

Typically, predictive coding accounts of sensorimotor processing propose that unpredicted information from the environment elicits larger activation in the relevant sensory areas in which it is represented (Rao and Ballard 1999; Friston et al. 2011). Predictions with higher precision are associated with larger prediction error signals. In our study, prediction error signals were reflected in stronger parieto-frontal

activations for the unpredicted movements when the used object's purpose was expected. Whereas higher activations for unpredicted sensory information are well explained and documented (Koster-Hale and Saxe 2013), the active inference account does not clearly specify how are expected and unexpected concepts reflected in brain activations. To understand the mechanism of conceptual-expectations, it is important to keep in mind that context can generate joint expectations for a variety of different objects (e.g., smelling can be achieved by using cheese, roses, or perfume). Therefore, objects that match the prior expectation are more likely to be processed than all the objects that mismatch the purpose. In accord with this proposal, we show greater activations in the PCC for perceived objects that matched the prior expectation regarding their purpose than for the objects that mismatched the prior expectation. This finding is in line with the active inference account (Friston et al. 2011) and could reflect the activation of "prediction units" which represent prior conceptual-expectation. Recent work (Koster-Hale and Saxe 2013) suggests that when the sensory input matches prior expectation, the "prediction units" that generate expectation should show robust activations. An alternative, though not mutually exclusive explanation is provided by the contextual association hypothesis (Bar 2007, 2009a, 2009b) that addresses functional/contextual relations between objects. The hypothesis proposes that objects with strong functional associations elicit stronger activation in conceptual brain regions, like the PCC. From this perspective, expected objects can be regarded as strongly associated with the primed context (e.g., smelling a rose).

In sum, stronger activation of the PCC signals the confirmation of expectation regarding the object's purpose, which might play a role in modulating precision of the lower level movement predictions. Importantly, our results are in line with the notion that activation and updating of perceptual predictions is contingent on more general prior expectations that facilitate action processing (Bar 2009a, 2009b; Clark 2013; Friston et al. 2011; Kveraga et al. 2011). It remains to be examined whether the hierarchical anticipatory mechanism may be generalizable to processing of speech (Gagnepain et al. 2012), learning and memory (Van Kesteren et al. 2012), and other fundamental neurocognitive functions (Clark 2013).

In sum, the current findings stress the role of a hierarchical predictive mechanism in understanding another individual's goal-directed behavior and suggest that the conceptual-expectations generated in the midline structures, including the PCC, affect the perceptuo-motor predictions involved in processing of bodily movements in the parieto-frontal network.

Notes

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