1 Title: Predictive coding account of action perception: Evidence from effective
2 connectivity in the Action Observation Network

3
4 Abbreviated title: Effective connectivity in the action observation network
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6 Authors:

7 Burcu A. Urgan

8 Department of Psychology, Bilkent University, Ankara, Turkey

9 Interdisciplinary Neuroscience Program, Bilkent University, Ankara, Turkey

10 Aysel Sabuncu Brain Research Center and National Magnetic Resonance Research

11 Center, Ankara, Turkey
12

13 Ayse P. Saygin

14 Department of Cognitive Science, University of California, San Diego, CA, USA

15 Neurosciences Graduate Program, University of California, San Diego, CA, USA
16

17 Corresponding author:

18 Burcu A. Urgan

19 Email: burcu.urgan@bilkent.edu.tr
20

21

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26

27 **Abstract**

28 Visual perception of actions is supported by a network of brain regions in the occipito-
 29 temporal, parietal, and premotor cortex in the primate brain, known as the Action
 30 Observation Network (AON). Although there is a growing body of research that
 31 characterizes the functional properties of each node of this network, the communication
 32 and direction of information flow between the nodes is unclear. According to the
 33 predictive coding account of action perception, this network is not a purely feedforward
 34 system but has feedback connections through which prediction error signals are
 35 communicated between the regions of the AON. In the present study, we investigated the
 36 effective connectivity of the AON in an experimental setting where the human subjects'
 37 predictions about the observed agent were violated, using fMRI and Dynamical Causal
 38 Modeling (DCM). We specifically examined the influence of the lowest and highest
 39 nodes in the AON hierarchy, pSTS and ventral premotor cortex, respectively, on the
 40 middle node, inferior parietal cortex during prediction violation. Our DCM results
 41 suggest that the influence on the inferior parietal node is through a feedback connection
 42 from ventral premotor cortex during perception of actions that violate people's
 43 predictions.

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50 1. INTRODUCTION

51 Over the last two decades, neurophysiological and neuroimaging studies in
 52 primates have identified a network of brain regions in occipito-temporal, parietal and
 53 premotor cortex that are associated with visual processing of actions, known as the
 54 Action Observation Network (AON, Rizzolatti & Craighero, 2004; Iacoboni & Dapretto,
 55 2006; Saygin, 2007; Caspers et al., 2010; Nelissen et al., 2011; Saygin, 2012). Although
 56 significant progress has been made in understanding the neural correlates of action
 57 perception, one open question in the field is how the nodes of this network communicate.
 58 This question is of particular importance to be able to specify neural mechanisms that go
 59 beyond neural correlation.

60 There has been theoretical work that provide a neuro-mechanistic account of
 61 action perception but empirical work that directly tests it is sparse. One such model by
 62 Kilner et al. (2007a; 2007b) proposes that the AON is a predictive system, following the
 63 principles of predictive coding (Friston, 2010). In this framework, information is
 64 processed throughout the AON by means of feedforward and feedback connections, in
 65 contrast to the classic formulation of the AON, which treats action perception strictly as a
 66 feedforward process (Giese and Poggio, 2003). More specifically, the middle node of the
 67 network, parietal node has reciprocal connections between the occipito-temporal node
 68 (the lower node in the hierarchy) and the premotor node (the higher node in the
 69 hierarchy) (Figure 1), which hypothetically enables the feedforward and feedback
 70 connections within the system.

Figure 1: Anatomical connectivity between the core nodes of the AON.

There is indeed empirical evidence for the anatomical connectivity of the brain regions that comprise the AON. Our knowledge of the anatomical connectivity patterns in the AON comes primarily from non-human primates. In the macaque monkey, area F5 of the premotor cortex and area PF of the inferior parietal lobule have reciprocal connections (Luppino, et al., 1999). PF also has reciprocal connections with a portion of the posterior superior temporal sulcus (pSTS) that is sensitive to biological movements (Seltzer & Pandya, 1994). Analogous connectivity patterns have been proposed in the human brain (Rushworth et al., 2006; Igelstrom and Graziano, 2017).

There is also a handful of experimental studies that provide support for predictive coding account of action perception. Kilner et al. (2004), using event-related brain

potentials, found that during action observation, the human brain generated a motor-preparation-like negative potential when the action was in a predictable context; no such potential was found when observation occurred within an unpredictable context. In a monkey neurophysiology study, Maranesi et al. (2014) provide direct evidence for predictive activity of visuo-motor neurons in premotor cortex and therefore it is considered to be a foundational step in supporting the predictive coding account of action understanding (Urgen and Miller, 2015). In another study, using an fMRI-adaptation paradigm, Saygin et al. (2012) found that the parietal node of the AON showed more adaptation to actions that violate predictions (via an agent who showed a mismatch between appearance and motion) than to actions that do not (via agent who shows a match between appearance and motion). The authors interpreted the differential adaptation in the parietal cortex for the prediction violations as reflecting prediction error signals generated due to a mismatch between the appearance and movement of the observed actor.

Due to the adaptation-based analysis in Saygin et al. (2012), it could not be determined whether the influence on parietal cortex came as a feedforward (bottom-up) modulation from earlier visual areas via pSTS, or as a feedback (top-down) modulation from premotor cortex in AON in the mismatch condition. The current study builds on this work and aims to reveal where that influence on parietal cortex might be generated from. Is it a top-down signal from premotor cortex or a bottom-up signal from pSTS? To address this question, we studied the effective connectivity patterns in the AON of the human brain and their modulation by the agent characteristics using functional magnetic resonance imaging (fMRI) and dynamical causal modeling (DCM) (Friston et al., 2003).

Specifically, we investigated the influence of two nodes of the AON, pSTS and premotor cortex over the third node, parietal cortex and how this influence was affected by the mismatch between the appearance and motion of the observed agent.

2. MATERIALS AND METHODS

The fMRI data used in the present study is the same as the one collected in Urgen et al. (2019). The methodological details are provided below.

2.1 Participants

27 subjects (12 females, 15 males) from the student community at the University of California, San Diego participated in the study. Data of 4 subjects were not included in the analysis due to excessive head movements (3 subjects) or technical problems during data acquisition (1 subject). The subjects had no history of neurological disorders and normal or corrected-to-normal vision. Informed consent was obtained in accordance with UCSD Human Research Protections Program. The subjects were paid \$25 for 1.5 hours participation in the study. All ROIs of interest for DCM analysis were identified in 18 subjects so those subjects were included in the DCM analysis.

2.2 Stimuli

Stimuli consisted of video clips of actions performed by 3 agents: a human agent, and the humanoid robot Repliee Q2 in two different appearances (human-like and robotic). These agents are referred here as Human, Android, Robot, respectively (Figure 2, also see Saygin et al. 2012; Urgen et al. 2013; 2019) for additional details about the stimuli).

Figure 2. Stimuli used in the action perception experiment. There were three agents: Human with biological appearance and biological motion (match between appearance and motion), Android with biological appearance and nonbiological motion (mismatch between appearance and motion), and Robot with nonbiological appearance and nonbiological motion (match between appearance and motion).

The agents differed from each other in terms of visual appearance and motion. The Human agent had biological appearance and biological motion, the Android agent had biological appearance and nonbiological motion, and the Robot agent had nonbiological appearance and nonbiological motion. So, in this setting both Human and Robot had a *match* between their appearance and motion (both biological and nonbiological, respectively), whereas Android had a *mismatch* between the appearance and motion. All the agents performed 8 different actions. The actions were comprised of a variety of actions included drinking from a cup, grasping an object, throwing a paper, wiping a table, nudging, turning the body to the right, handwaving, and talking (for introducing herself).

146 **2.3 Procedure**

147 Each participant was given exactly the same introduction to the study and the
148 same exposure to the videos as prior knowledge can induce biases against artificial agents
149 (Saygin and Cicekli, 2002). Before starting fMRI scans, subjects were shown each video
150 and were told whether each agent was a human or a robot (and thus were not uncertain
151 about the identity of the agents during the experiment). We recorded fMRI BOLD
152 response as subjects watched 2 sec action clips in a total of 8 runs. In each run, the
153 experiment had a block design in which blocks consisted of video clips of one agent type
154 (Human, Android, or Robot, see Figure 2). The experiment had 18 stimuli blocks (6
155 Human, 6 Android, 6 Robot) and they were presented in a pseudo-randomized order
156 ensuring that all order combinations were presented (i.e. H-A-R, H-R-A, A-H-R, A-R-H,
157 R-H-A, R-A-H). A rest block followed the presentation of the three blocks of agents.
158 There, subjects fixated on a cross for a time interval varying between 8.1 sec and 13.5
159 sec. Each block had 9 trials (8 different actions and repetition of a randomly chosen
160 action once) with 0.1 sec inter-stimulus interval in between the trials. Each subject was
161 presented a different order of blocks and of stimuli within each block. In order to keep
162 subjects' attention throughout the experiment, a one-back task was performed in which
163 subjects pressed a button whenever a movie was repeated.

164 **2.4 Image acquisition, preprocessing and first-level analysis**

165 We scanned our subjects at the Center for fMRI at UC San Diego using the 3T
166 GE MR750 scanner (TR = 2.7 sec, TE = 30, Flip angle = 90, number of slices = 35, voxel
167 size = 3mm x 3mm x 3mm, 152 volumes in each run, sequential acquisition). The stimuli
168 were presented on a projector through a mirror mounted in the head cover in the scanner.

169 First, the fMRI data of each subject were pre-processed with standard procedures
 170 including motion correction, slice-time correction, normalization, and smoothing using
 171 the SPM8 software. Then, two different first-level analyses were done using general
 172 linear model (GLM). In the first analysis, each agent type (Human, Android, Robot) as
 173 well as the rest blocks (fixation) were modeled as a separate condition and beta images
 174 were generated for these conditions. This analysis was done to identify the overall
 175 activity patterns and determine the ROIs of the AON. The second analysis was done to
 176 investigate the modulations in the AON via dynamical causal modeling (See Section 2.6).
 177 In the second analysis, we defined two conditions: The first condition was defined as
 178 *Actions* and consisted of actions of all three agents (Human, Android, Robot) to
 179 investigate the modulations of the connections by any action stimulus regardless of agent.
 180 The second condition was defined as the *Mismatch* condition, and consisted of the actions
 181 only by the Android, which featured a mismatch between appearance and motion, to
 182 investigate the modulations of the connections by the Mismatch condition. Motion
 183 parameters generated in the preprocessing stage were used as regressors in both analyses.

184 **2.5 Identification of ROIs**

185 We identified the ROIs of the AON by contrasting the overall activation patterns
 186 for all stimuli conditions compared to fixation ($p < 0.001$ uncorrected, cluster threshold k
 187 $= 5$ voxels) using the first first-level analysis for each subject (described in Section 2.4
 188 above). We chose the central voxel of the activation in each node of the AON and
 189 extracted a sphere ROI that covers the activation pattern. We did this for all 18 subjects
 190 for whom we identified all ROIs of interest. The ROI time series data was then extracted
 191 using eigenvariate (threshold of $p < 0.05$) as a sphere with 4 mm radius.

192

193 **2.6 Specification of the network models**

194 In order to investigate whether a mismatch between appearance and motion of an
195 agent during action perception was mediated through a bottom-up process from pSTS to
196 inferior parietal cortex, or as a top-down process from ventral premotor cortex to inferior
197 parietal cortex, we analyzed our fMRI data with dynamical causal modeling (DCM).

198 Dynamical causal modeling (DCM) is an effective connectivity technique to
199 estimate the directed functional connectivity between different regions of interest with
200 fMRI (Friston et al., 2003; Penny et al., 2004). DCM consists of two stages: Model
201 specification and estimation, and model selection. In the model specification and
202 estimation stage, several model architectures are specified based on the known anatomy
203 between brain regions of interest and the hypothesis about how the connections might be
204 modulated by the experimental manipulations. Three parameters are estimated: 1)
205 Intrinsic connections between brain regions, 2) How the intrinsic connections are
206 modulated by experimental manipulations, 3) The extrinsic input strength into the
207 system. In the model selection stage, Bayesian Model Selection (BMS) procedure is used
208 to determine the most likely model that generated the observed data. In this procedure,
209 each model architecture in the model space is given a probability for explaining the
210 observed data. The model that has the highest probability is then considered to be the
211 “winning” or the most optimal model.

212 To test our hypothesis, we constructed 3 models that consisted of the main three
213 ROIs of the AON, namely pSTS, the inferior parietal node, and the ventral premotor node
214 (See the coordinates listed in Table 2) for each subject and in each hemisphere. To

215 constrain the model space, in each of these models, the intrinsic connections between the
 216 ROIs were informed by the known anatomical connections between the regions. As such,
 217 pSTS and the parietal node, and the parietal node and the premotor node had reciprocal
 218 connections between each other (Figure 3A). Furthermore, in all models, pSTS was
 219 considered to be the node where the visual input entered the system, and all intrinsic
 220 connections were modulated by the observation of actions (*Action* condition, see Section
 221 2.4). In other words, the observation of actions was assumed to evoke activity in pSTS
 222 first (input to the system), and then subsequently propagated to parietal and premotor
 223 cortex based on the known anatomical connections. After the first feedforward flow of
 224 information from a lower area to a higher area, feedback from a higher area to a lower
 225 area occurred in all models.

226 The three models differed with regard to which connections were modulated by
 227 the *Mismatch* condition (See Section 2.4, Figure 3B). The first model posits that
 228 influence on parietal cortex activity is through connections from pSTS to parietal cortex,
 229 i.e., a bottom-up modulation (Model 1). The second model posits that the influence on
 230 parietal cortex is through feedback from ventral premotor cortex, i.e., a top-down
 231 modulation (Model 2). A third possibility is that the influence would be expressed
 232 through both pSTS and premotor cortex connections (Model 3).

Figure 3: DCM models tested in the model space. (A) The DCM model that forms the basis for all tested models in the model space in (B). There are reciprocal intrinsic connections between pSTS and parietal node, and the parietal node and the premotor node informed by anatomy (red arrows). The input to the system is assumed to enter to the AON through pSTS since pSTS gets information from the visual cortex (blue dashed arrow). All the intrinsic connections are modulated by observation of actions (dashed blue lines). (B) The model space that consists of three models that correspond to our hypothesis about how the mismatch condition might modulate the intrinsic connections. Model 1 tests a bottom-up modulation from pSTS to parietal node, Model 2 tests a top-down modulation from premotor node to parietal node, and Models 3 tests both a bottom-up and a top-down modulation.

244 To identify the winning model, i.e. the model that explains that data best,
245 Bayesian Model Selection (BMS) was used. This method determines a probability for
246 each model, known as the exceedance probability, which is the probability that a model is
247 more likely than any other model tested in the model space.

248 3. RESULTS

249 3.1 Brain Regions that are involved in Visual Processing of Actions

250 In order to identify the brain regions that were involved in visual processing of
251 actions, we ran the contrast between the observation of actions of all agents (Human,
252 Android, Robot) and the fixation condition. This contrast revealed the activation in early
253 visual cortex extending dorsally to lateral occipital cortex (LOC) and ventrally to the
254 inferior temporal cortex, as well as the core areas for AON, namely pSTS, parietal
255 regions in the anterior part of the intra-parietal sulcus (AIP) and inferior and superior
256 parts of the parietal lobe, and dorsal and ventral parts of the premotor cortex, all
257 bilaterally ($p < 0.001$, cluster level 5) (Figure 4; Table 1 for the coordinates of all
258 activations).

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261 **Figure 4:** Whole brain GLM analysis with the contrast All Agents (Human, Android, Robot) – Fixation (p
262 < 0.001 , cluster threshold $k = 5$ voxels) at the group level. The contrast revealed activation in early visual
263 areas extending dorsally to lateral occipital cortex (LOC), and ventrally to inferior temporal cortex, pSTS,
264 parietal cortex, and premotor cortex dorsally and ventrally in both hemispheres. See the coordinates in
265 Table 1.

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Table 1: MNI Coordinates of the peak voxels of the brain regions involved in visual processing of actions based on the All Agents-Fixation contrast in the whole brain GLM analysis (Figure 3).

MNI coordinates				
x	y	z	Anatomical Name	Brodmann Area
-34	-92	0	Middle occipital gyrus (left)	BA 17
-26	-92	-10	Inferior occipital gyrus (left)	BA 18
-48	-80	-2	Middle occipital gyrus (left)	BA 19
48	-74	-2	Inferior temporal gyrus (right)	BA 19
40	-84	-8	Inferior occipital gyrus (right)	BA 19
22	-94	-6	Sub-gyral (right)	BA 18
42	2	56	Middle frontal gyrus (right)	BA 6
50	34	34	Middle frontal gyrus (right)	BA 9
46	10	30	Inferior frontal gyrus (right)	BA 9
-34	-58	50	Superior parietal lobule (left)	BA 39
38	-56	52	Inferior parietal lobule (right)	BA 40
32	-68	28	Sub-gyral (right)	BA 39
-44	0	56	Middle frontal gyrus (left)	BA 6
-42	-2	38	Middle frontal gyrus (left))	
-60	6	32	Inferior frontal gyrus(left)	BA 6
-6	12	50	Medial frontal gyrus (left)	BA 6
28	-6	-22	Amygdala (right)	
-12	26	60	Superior frontal gyrus (left)	BA 6
8	-22	68	Medial frontal gyrus (right)	BA 6
38	-26	58	Precentral gyrus (right)	BA 4

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In order to deal with the expansion of model space with increasing number of ROIs and constrain the model space used in the effective connectivity analysis, we extracted ROIs from pSTS, inferior parietal, and ventral premotor cortex in each subject, and excluded the areas in early visual areas. The coordinates of the central voxels of the ROIs averaged over subjects are displayed in Table 2. On average, subjects were 96 percent accurate in the behavioral task.

Table 2: The MNI coordinates of central voxels of the ROIs used in the DCM analysis averaged across subjects. pSTS: posterior superior temporal sulcus, STG: superior temporal gyrus, MTG: middle temporal gyrus, IPL: inferior parietal lobule, IFG: inferior frontal gyrus. Values in parenthesis under x, y, z coordinates indicate the standard error of the mean.

Average MNI coordinates of the central voxels of ROIs in DCM analysis				
	Left hemisphere		Right hemisphere	
Node names in DCM	x y z (Standard error of mean)	Anatomical name/Brodmann Area	x y z (Standard error of mean)	Anatomical name/Brodmann Area
pSTS	-50 -53 7 (1 2 1)	STG/BA 39	53 -44 8 (1 2 1)	MTG/BA 22
Parietal cortex	-37 -42 44 (1 1 1)	IPL/BA 7	37 -42 47 (1 1 1)	Subgyral/BA 7
Premotor cortex	-44 6 29 (1 1 1)	IFG/BA 6	47 9 28 (1 2 1)	IFG/BA 44

3.2 Effective Connectivity with DCM and Model Selection with BMS

The three DCMs included the three ROIs: pSTS, the inferior parietal node, and the premotor node (ventral premotor cortex). The intrinsic connections included the reciprocal connections between pSTS and the parietal node, and the parietal node and the ventral premotor cortex. The input into the system was considered to come from pSTS.

291 Observation of all actions was considered to modulate all intrinsic connections (defined
292 by the *Action* condition, see Section 2.4), and the *Mismatch* condition was considered to
293 modulate either the pSTS-parietal connection (Model 1), premotor-parietal connection
294 (Model 2), or both of these connections (Model 3).

295 BMS analysis on the three DCMs showed that Model 2 was the winning (optimal)
296 model in both hemispheres, whose probability was 0.43 in the left and 0.50 in the right
297 (Figure 5). The next best model was Model 1 whose probability was 0.32 on the left, and
298 0.36 on the right. The least likely model, Model 3 had a probability of 0.25 on the left,
299 and 0.14 on the right.

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301 **Figure 5:** The exceedance probability of each model in the model space. Image on the left shows the
302 results of the model testing in the left hemisphere, and the one on the right shows the results of the right
303 hemisphere. In both hemispheres, Model 2 has the highest probability.
304

305 The intrinsic connection strengths between the ROIs in the winning model, Model
306 2, are listed in Table 3. All connection strengths were found to be significant (greater
307 than 0 by a one-sample t-test, $p < 0.0001$) confirming the anatomical connectivity of each
308 pair of regions. In addition, the connection directed from pSTS to the parietal node was

estimated to be stronger than the other three connections (parietal to pSTS, parietal to premotor, premotor to parietal) both in the left and the right hemisphere.

Table 3: The parameters of the intrinsic connectivity that begins with the endogenous activity of actions in the winning model (Model 2) in both hemispheres. The values in the table indicate the mean connection strength across all subjects.

	FROM						
TO		Left hemisphere			Right hemisphere		
		pSTS	Parietal	Premotor	pSTS	Parietal	Premotor
	pSTS	-0.4962	0.0382	-	-0.4964	0.0342	-
	Parietal	0.2016	-0.4994	0.0069	0.2168	-0.4994	0.0071
	Premotor	-	0.0449	-0.5000	-	0.0461	-0.5000

On the other hand, in the winning model Model 2, the modulatory effects of *Actions* on all four connections were found to be significant (greater than 0 by a one-sample t-test, $p < 0.0001$). The strength of the modulatory effects of *Actions* is shown in Table 4 and displayed on the right hemisphere in Figure 6 together with input strength. The connection between pSTS and the parietal node was modulated most strongly. The modulatory effect of the Mismatch condition on the premotor-parietal connection was 0.0003 on both hemispheres. The input strength was -0.0058 on the left hemisphere, and -0.0057 on the right hemisphere.

Figure 6: Modulatory connection strengths in the winning model, Model 2 across subjects (only right hemisphere is shown for display purposes). The mean values for action modulations for both hemispheres are also listed in Table 4. Modulations by actions are shown by the blue dashed lines. Modulation by the mismatch condition is shown by the red dashed line. All connection strengths were significantly different from 0 (with a one-sample t-test, $p < 0.0001$).

Table 4: The parameters of the modulatory activity of actions in the winning model (Model 2) in both hemispheres. The values in the table indicate the mean connection strength across all subjects.

TO	FROM						
		Left hemisphere			Right hemisphere		
		pSTS	Parietal	Premotor	pSTS	Parietal	Premotor
pSTS		-	0.0095	-	-	0.0077	-
Parietal		0.0798	-	0.0005	0.0850	-	0.0005
Premotor		-	0.0121	-	-	0.0121	-

337 4 DISCUSSION

338 The brain regions that are involved in visual processing of actions are relatively
 339 well-established in cognitive neuroscience (Caspers et al., 2010, Saygin, 2012). However,
 340 how the information flows between these regions have been little understood. In the
 341 present study, we aimed to estimate the effective connectivity patterns between the core
 342 nodes of the Action Observation Network and how these connections were modulated by
 343 prediction violations during action perception. Our study was primarily motivated by the
 344 findings of Saygin et al. (2012), who reported that the parietal node of the AON showed
 345 differential activity during observation of actions which were performed by an agent who
 346 possessed a mismatch between appearance and motion (a biological appearance but
 347 mechanical motion) compared to other agents who possessed a match between
 348 appearance and motion (biological appearance and motion or mechanical appearance and
 349 motion). Within the predictive coding account of action perception (Kilner et al. 2007a;
 350 2007b), one question that has been of interest to us was whether that differential activity
 351 in parietal cortex was a top-down effect from premotor cortex or a bottom-up effect from
 352 pSTS. The current study addressed this question using fMRI and DCM.

353 We constructed three models to test our hypothesis. First of all, informed by well-
 354 known anatomy in the primate brain, in all these models, we created reciprocal intrinsic
 355 connections between pSTS and the inferior parietal node, and the inferior parietal node
 356 and the ventral premotor node. The input into the system was considered to enter from
 357 pSTS, which was a reasonable assumption given the involvement of pSTS in visual
 358 analysis of form and motion information in observed actions (Vangeneugden et al. 2009;
 359 2011; Urgen et al., 2019). In addition, in all these models, we assumed that observation of

actions modulated all intrinsic connections. We then constructed three specific models that corresponded to our hypotheses: A first model in which the connection from pSTS to parietal cortex was modulated, a second model in which the connection from the premotor cortex to the parietal cortex was modulated, and a third model in which both connections were modulated by the mismatch condition (the agent that exhibited a mismatch between appearance and motion). Our results show that the most likely model that best explains the data is a model in which the connection from the premotor cortex to the parietal cortex was modulated, which indicates a top-down influence.

Examination of the parameter estimates of the optimal model shows that all of the intrinsic connections were significant, confirming the well-known anatomy between these regions (Luppino, et al., 1999; Seltzer & Pandya, 1994; Rushworth et al., 2006). The strongest intrinsic connectivity was between the pSTS and the inferior parietal node. On the other hand, all of the intrinsic connections were modulated significantly by the observation of actions, which is consistent with an earlier DCM study of action observation (Sasaki et al., 2012). These results suggest that action-related information is processed via both feedforward and feedback connections in the AON. On the other hand, the mismatch between appearance and motion of an observed agent during action perception was likely mediated primarily via a feedback connection from the premotor to the parietal node of the AON.

These results provide support for the predictive coding account of action perception (Kilner et al., 2007a; 2007b), which proposes that there are reciprocal connections between the three levels of the AON, and prediction error signals are communicated via the feedback connections. Our data shows that actions are not only

383 processed by a network that has feedforward and feedback connections consistent with
 384 previous work (Sasaki et al., 2012; Maffei et al. 2015; Gardner et al., 2015; Cardellicchio
 385 et al., 2018; Sokolov et al., 2018) but also provides evidence that in the case of prediction
 386 violations (e.g. when a moving agent exhibits a mismatch between appearance and
 387 motion), the premotor node of the AON likely sends a feedback signal to the inferior
 388 parietal node in the lower part of the hierarchy, which might indicate a prediction error
 389 signal (Saygin et al., 2012).

390 However, some caveats must be noted. BMS is a Bayesian approach, which
 391 assigns a probability to each model tested in the model space and constrained by the
 392 experimental design. Future studies should test the generality of this model during action
 393 observation under different task demands. For instance, the mismatch between the two
 394 visual cues, appearance and motion is a particular case where predictions are violated
 395 during action perception. Novel prediction paradigms in which there are mismatches
 396 between different visual cues, multi-sensory cues, or even cognitive cues (e.g. as in
 397 Costantini et al., 2005; Koelewijn et al., 2008; Stapel et al., 2010) should be tested in
 398 future studies of action observation with effective connectivity techniques.

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