



Where and how our brain represents the temporal structure of observed action

R.M. Thomas^{a,b,1}, T. De Sanctis^{a,d,1}, V. Gazzola^{a,c,2,*}, C. Keysers^{a,c,2,*}

^a The Netherlands Institute for Neuroscience, An Institute of the Royal Netherlands Academy of Arts and Sciences (KNAW), Amsterdam, the Netherlands

^b Department of Psychiatry, Academic Medical Center, University of Amsterdam, Amsterdam, the Netherlands

^c Brain & Cognition, Department of Psychology, University of Amsterdam, Amsterdam, the Netherlands

^d PharmAccess Foundation, Amsterdam, Netherlands

ARTICLE INFO

Keywords:

Action observation
EEG
fMRI
ISC
Hebbian learning

ABSTRACT

Reacting faster to the behaviour of others provides evolutionary advantages. Reacting to unpredictable events takes hundreds of milliseconds. Understanding where and how the brain represents what actions are likely to follow one another is, therefore, important. Everyday actions occur in predictable sequences, yet neuroscientists focus on how brains respond to unexpected, individual motor acts. Using fMRI, we show the brain encodes sequence-related information in the motor system. Using EEG, we show visual responses are faster and smaller for predictable sequences. We hope this paradigm encourages the field to shift its focus from single acts to motor sequences. It sheds light on how we adapt to the actions of others and suggests that the motor system may implement perceptual predictive coding.

1. Introduction

The capacity to perceive and predict actions performed by others is fundamental to proper social interactions. Over the past few decades, much research attention has been devoted to identifying the neural mechanisms that underlie the processing of simple acts such as grasping, reaching, breaking, and performing simple gestures. Electrophysiological work on non-human primates has identified that some of the neurons active while participants perform simple acts are also active when observing (or hearing) similar acts performed by others. These neurons, called ‘mirror neurons’, were originally identified in ventral premotor region F5 and in the rostral inferior parietal region PF/PFG (Gallese et al., 1996; Umiltà et al., 2001; Kohler et al., 2002; Keysers et al., 2003; Fogassi et al., 2005). Later studies have described neurons with such mirroring properties in (a) somatosensory cortices (particularly in SII and adjacent sectors of SI Hihara et al., 2015), (b) the dorsal premotor cortex (Cisek and Kalaska, 2004; Tkach et al., 2007), and (c) to a lesser extent, the primary motor cortex (Dushanova and Donoghue, 2010; Kraskov et al., 2014; Vigneswaran et al., 2013). Our current estimate of the mirror neuron system – i.e. the network of brain regions with neurons rendered active during both the observation and performance of specific actions –

comprises all these regions. Whether such mirror neurons exist elsewhere in the primate brain remains unanswered, as systematic experiments to examine the issue remain to be carried out. The firing of individual mirror neurons contains information that will permit accurate classification of the acts performed by others (C Keysers et al., 2003). This work has led to the idea that isolated observed or heard acts are processed, at least in part, by recruiting somatosensory-motor representations of the monkey's own actions (Gallese et al., 2004; Rizzolatti and Sinigaglia, 2010; Umiltà et al., 2001). A large number of neuroimaging studies in humans have identified an *action observation network* triggered by the observation of such simple acts (for ALE meta-analyses of these studies see for instance Caspers et al., 2010; Grosbras et al., 2012; Molenberghs et al., 2012). A smaller number of studies have tested the same participants during both their observation and execution of manual actions. These studies identified a network of voxels involved in both conditions (e.g. Arnstein et al., 2011; Buccino et al., 2004; Dinstein et al., 2007; Filimon et al., 2007; Gazzola and Keysers, 2009; Grèzes et al., 2003; Simos et al., 2017; Valchev et al., 2016). We shall henceforth refer to this network as the Action Observation-Execution Network (AOEN). The AOEN network includes (a) the presumed human homologue of the brain areas in which mirror neurons have been found in monkeys (vPM, dPM,

* Corresponding authors. Netherlands Institute for Neuroscience, Meibergdreef 47, 1105BA Amsterdam, the Netherlands.

E-mail addresses: v.gazzola@nin.knaw.nl (V. Gazzola), c.keysers@nin.knaw.nl (C. Keysers).

¹ Equal contributions.

² Equal contributions.

SI, SII, PF/PFG) and (b) a number of regions that have not yet been systematically explored for the presence of mirror neurons in monkeys (in particular, the cerebellum, SPL, SMA and regions of the visual cortex such as V5 and EBA). Pattern classification analyses have confirmed that the pattern of brain activity in premotor, inferior parietal and somatosensory cortices does contain information that could help the organism perceive which motor act someone else performed (Etzel et al., 2008; Oosterhof et al., 2010). Disturbing activity in the somatosensory-motor nodes of this AOEN (SI, IPL, PM) leads to deficits in the processing of observed actions (for recent reviews see Avenanti et al., 2013; Keysers et al., 2018; Urgesi et al., 2014). Together, these findings suggest that humans also recruit brain regions associated with the planning, execution and somatosensation of their own actions in their perception and interpretation of the actions of others.

In contrast, we know very little about **where** and **how** the brain represents knowledge and expectations about **sequences** of acts, e.g. preparing breakfast (Grafton and Hamilton, 2007; Kilner and Frith, 2008; Thioux et al., 2008). Intelligent participation in coherent action sequences inevitably requires information that goes beyond the sum of the knowledge about the individual acts that go into their making. Representing a sequence of acts entails representing the order in which the acts were performed. Such *ordinal* information is critical to predicting actions that people are likely to perform as the follow up to a previous step. This prediction, in turn, is crucial to an intelligent agent's proactive planning of reactions to the that follow up. In this paper, we shall present the experimental evidence we have gathered about both the areas and the manner in which this knowledge is represented in the brain.

To explore **where** the brain encodes sequence level information, we localized regions responding differently to acts in a logical sequence (e.g. grasping a bun, cutting the bun, buttering the bun) and in a random sequence. Some scientists (e.g. Brass et al., 2007; Caramazza et al., 2014; Kilner and Frith, 2008) have argued that such higher-level information is more likely to be represented in the Theory of Mind (ToM) network than in the motor system. Systematic reviews of studies looking at reasoning about the mental states of others have revealed a core network composed of the medial prefrontal and rTPJ that are consistently activated whenever participants are reasoning about mental states of others irrespective of the task- and stimulus format (Mar, 2011; Schurz et al., 2014). There are some, including us, who suggest that the AOEN could represent sequence-level information. We base our suggestion on insights from experiments on monkeys showing that mirror neurons in the motor system are sensitive to expectations about upcoming actions (Fogassi et al., 2005; Umiltà et al., 2001). This is also in line with observations that premotor cortices do represent sequences of stimuli in other domains (Fiebach and Schubotz, 2006; Schubotz and von Cramon, 2001; Schubotz et al., 2004). When we act, we can see our own actions unfold in our perceptual space, so we can surmise that Hebbian learning in the synapses mutually connecting our visual and motor systems would encode the transitional probabilities across individual motor acts, and thereby enable our AOEN to represent sequence-level information and anticipation in a predictive coding framework (Keysers and Gazzola, 2014). Indeed the possibility that the AOEN is involved in such prediction is corroborated by recent experiments that show that virtual lesions to premotor cortices (Avenanti et al., 2017; Makris and Urgesi, 2015) or neurological lesions to the premotor, somatosensory or inferior parietal cortices (de Wit and Buxbaum, 2017) interferes with our ability to predict actions in a sequence.

Lerner et al. (2011) suggests a powerful experimental method to investigate this issue. They took a story and presented it to participants once in its intact form, or then after cutting it at the spaces between words and randomizing the order of the words. If brain regions are sensitive only to word-level information, randomizing the order of the words in the story should not alter brain activity. The hypothesis was that, if brain regions respond to higher, sentence- or paragraph-level information, then, randomizing the order of the words should destroy that information and reduce the efficacy of brain activity. Brain activity

was then analysed using inter-subject correlations (ISC) (Hasson et al., 2012). ISC maps information about a stimulus in the brain in a model free fashion based on a simple logic. If a voxel has no information about a stimulus, its activity reflects spontaneous activity and will not be correlated in time with that of other participants exposed to the same stimulus. If a voxel's activity is strictly determined by a stimulus, activity across witnesses of the stimulus will be similar, and the inter-subject correlation will be significant. If so, the higher the temporal correlation between subjects with respect to a voxel, the more evidence we have of that voxel's ability to contain information about the stimulus. By comparing ISC of the intact and scrambled sentences, Lerner et al. identified brain regions that show evidence of significant additional information/correlation when sentence level information was preserved, i.e., when the sentences were presented intact, than when sentence level information was degraded, i.e., when the words were presented in a random order.

Here we adapted this approach to localize brain regions containing action sequence-level information. We recorded movies of routine actions lasting approximately 1 min (Table 1). We then measured brain activity using fMRI in 22 participants while they viewed intact movies that contain sequence- and act-level information. Then we presented the same movies disjointed at the points of transition between acts, and with the order of the acts randomized. We also measured brain activity while participants viewed these scrambled movies containing the same act-level information, but with perturbed sequence-level information (Fig. 1). We then localized brain regions that had significantly different ISC values for the intact and scrambled movies to identify regions involved in processing sequence-level information. It is important to note that not finding a region in this contrast does not mean that region has no role in encoding sequence-level information. In addition to the usual limitations regarding negative findings, this is because ISC identifies activations occurring at the same location and time across participants, and thus focuses on stimulus-locked processes (Hasson et al., 2012; Stephens et al., 2013). If different participants encode the sequence of the overall actions (e.g. making breakfast) at different points along the sequence, this would evade the ISC analysis, and a region could then be involved in encoding this form of sequence-level information without showing increased ISC. We will therefore supplement ISC analyses with analyses exploring average activity levels across the sequences to shed light on activity that is consistent in location across individuals but not in timing. We generated a simple excel sheet to illustrate the difference between ISC and a traditional block-design GLM (bGLM, see Supplementary Materials – ISC bGLM differences). The ISC detects stimulus-locked fluctuations of activity that occur at the same time for all

Table 1

List of sequences used as stimuli with total duration in seconds and number of motor acts.

	Action	Seconds	Acts
1	Inflating and tying a balloon.	51	27
2	Making a paper boat.	94	32
3	Preparing bread with butter and jam.	79	40
4	Sewing a button.	66	42
5	Writing a gift card.	83	39
6	Rolling a cigarette.	72	30
7	Arranging flowers in a vase.	82	39
8	Framing a picture.	112	39
9	Cleaning spectacles.	69	38
10	Cleaning a laptop screen.	46	28
11	Sending a letter.	42	34
12	Replacing battery in a torch.	51	27
13	Applying nail polish.	49	23
14	Squeezing oranges.	62	40
15	Sharpening a pencil.	83	44
16	Replacing a pillow cover.	44	35
17	Removing nail polish.	64	32
18	Preparing a sandwich.	77	27
19	Toasting bread.	65	30
20	Folding a shirt.	38	20

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