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Research Report

Distinct sensitivities of the lateral prefrontal cortex and extrastriate body area to contingency between executed and observed actions

Akihiro T. Sasaki [a,b,c,d,1], *Yuko Okamoto* [e,f,j,1], *Takanori Kochiyama* [e], *Ryo Kitada* [g,*] and *Norihiro Sadato* [a,h,i]

[a] *National Institute for Physiological Sciences, Okazaki, Aichi, Japan*
[b] *Pathophysiological and Health Science Team, RIKEN Center for Life Science Technologies, Kobe, Hyogo, Japan*
[c] *Laboratory for Pathophysiological and Health Science, RIKEN Center for Biosystems Dynamics Research, Kobe, Hyogo, Japan*
[d] *Health Evaluation Team, RIKEN Compass to Healthy Life Research Complex Program, Kobe, Hyogo, Japan*
[e] *ATR-Promotions, Brain Activity Imaging Center, Kyoto, Japan*
[f] *Research Center for Child Mental Development, University of Fukui, Yoshida, Fukui, Japan*
[g] *School of Social Sciences, Nanyang Technological University, Singapore*
[h] *Division of Physiology, Department of Life Science, The Graduate University of Advanced Study (SOKENDAI), Okazaki, Aichi, Japan*
[i] *Biomedical Imaging Research Center, University of Fukui, Yoshida, Fukui, Japan*
[j] *Advanced Telecommunications Research Institute International, Sorakugun, Kyoto, Japan*

ARTICLE INFO

Article history:
Received 11 January 2018
Reviewed 10 February 2018
Revised 23 April 2018
Accepted 2 August 2018
Action editor Gereon Fink
Published online 27 August 2018

Keywords:
Social contingency
Being imitated
Agency

ABSTRACT

Detecting relationships between our own actions and the subsequent actions of others is critical for our social behavior. Self-actions differ from those of others in terms of action kinematics, body identity, and feedback timing. Thus, the detection of social contingency between self-actions and those of others requires comparison and integration of these three dimensions. Neuroimaging studies have highlighted the role of the frontotemporal network in action representation, but the role of each node and their relationships are still controversial. Here, we conducted a functional MRI experiment to test the hypothesis that the lateral prefrontal cortex and lateral occipito-temporal cortex are critical for the integration processes for social contingency. Twenty-four adults performed right finger gestures and then observed them as feedback. We manipulated three parameters of visual feedback: action kinematics (same or different gestures), body identity (self or other), and feedback timing (simultaneous or delayed). Three-way interactions of these factors were observed in the left inferior and middle frontal gyrus (IFG/MFG). These areas were active

Abbreviations: CDM, contingency detection module; EBA, extrastriate body area; SNC, Self/No-Delay/Concordant; ONC, Other/No-Delay/Concordant; SND, Self/No-Delay/Discordant; OND, Other/No-Delay/Discordant; SDC, Self/Delay/Concordant; ODC, Other/Delay/Concordant; SDD, Self/Delay/Discordant; ODD, Other/Delay/Discordant; IFG, inferior frontal gyrus; MFG, middle frontal gyrus; SPL, superior parietal lobule; PreCG, precentral gyrus; ITG, inferior temporal gyrus; MTG, middle temporal gyrus; PostCG, postcentral gyrus; SFG, superior frontal gyrus; IPL, inferior parietal lobule; ASD, autism spectrum disorders.

* *Corresponding author*. School of Social Sciences, Nanyang Technological University, 14 Nanyang Avenue, 637332, Singapore.
E-mail address: ryokitada@ntu.edu.sg (R. Kitada).

[1] These authors contributed equally to the work of this manuscript.

https://doi.org/10.1016/j.cortex.2018.08.003

Body ownership
Action observation network

when self-actions were directly fed back in real-time (i.e., the condition causing a sense of agency), and when participants observed gestures performed by others after a short delay (i.e., the condition causing social contingency). In contrast, the left extrastriate body area (EBA) was sensitive to the concordance of action kinematics regardless of body identity or feedback timing. Body identity × feedback timing interactions were observed in regions including the superior parietal lobule (SPL). An effective connectivity analysis supported the model wherein experimental parameters modulated connections from the occipital cortex to the IFG/MFG via the EBA and SPL. These results suggest that both social contingency and the sense of agency are achieved by hierarchical processing that begins with simple concordance coding in the left EBA, leading to the complex coding of social relevance in the left IFG/MFG.

1. Introduction

Humans can recognize the relationships between self-actions and their consequences during social interactions—a cause-effect representation referred to as social contingency (Gergely, 2001; Nadel, 2002). Social contingency is considered a basic element of the development of social communication skills (Contaldo, Colombi, Narzisi, & Muratori, 2016) and is known to influence the social behavior of adults (Ashton-James, van Baaren, Chartrand, Decety, & Karremans, 2007; van Baaren, Holland, Kawakami, & van Knippenberg, 2004). Although several studies have examined the neural mechanisms underlying social contingency detection in infants (Reid, Striano, & Iacoboni, 2011; Saby, Marshall, & Meltzoff, 2012) and adults (Decety, Chaminade, Grèzes, & Meltzoff, 2002; Guionnet et al., 2012; Kuhn et al., 2010; Okamoto et al., 2014), these mechanisms remain poorly understood. In the present study, we investigated the neural substrates underlying contingency detection between observed and executed actions.

To explain the development of social contingency detection in children, Gergely and Watson (1999) postulated the presence of a "contingency detection module (CDM)", which functions to establish the primary representation of the bodily self as well as the subsequent orientation toward reactive social objects. This module is innately set to preferentially explore perfect response-contingent stimulation. This perfect contingency includes the relationship between a self-action and its simultaneous visual feedback. Around 3 months of age, the CDM is "switched" toward a preference for less-than-perfectly contingent actions of others, such as the recognition of being imitated (Bahrick & Watson, 1985; Gergely & Watson, 1999). This hypothesis suggests that common mechanisms are involved in perfect and less-than-perfect social contingencies.

Both perfect and less-than-perfect contingencies involve specific relationships between the self-produced and subsequently observed actions of oneself and others. For instance, in perfect contingency, we observe the same action kinematics of our own body at the same timing as the executed action, which leads to the sense of agency. On the other hand, in the case of less-than-perfect contingency (e.g., being imitated), we observe another's body movement only after the execution of the self-action, although the action kinematics of the two movements are the same. Thus, contingency detection requires comparison of executed and observed actions in terms of action kinematics, body identity (self or other), and timing (simultaneous or delayed), as well as the integration of signals reflecting the results of such comparisons. If there is a neural substrate corresponding to the CDM, it should be involved in integrating signals that reflect different aspects of the output/input relationship in both perfect and less-than-perfect contingencies.

Several neuroimaging and electrophysiological studies have aimed to identify the brain networks activated during both action execution and observation (Caspers, Zilles, Laird, & Eickhoff, 2010; Gazzola & Keysers, 2009; Iacoboni & Dapretto, 2006; Molenberghs, Cunnington, & Mattingley, 2012). Previous functional magnetic resonance imaging (fMRI) studies have indicated that the lateral prefrontal cortex (LPFC) and lateral occipito-temporal cortex (LOTC) are involved in the sense of agency (David et al., 2007; Sperduti, Delaveau, Fossati, & Nadel, 2011) and imitation recognition (Decety et al., 2002; Guionnet et al., 2012; Okamoto et al., 2014). The LOTC receives motor input (Astafiev, Stanley, Shulman, & Corbetta, 2004; Orlov, Makin, & Zohary, 2010), while a portion of the extrastriate body area (EBA) within the lateral occipito-temporal cortex is sensitive to imitation (Okamoto et al., 2014) and has been associated with the sense of agency (David et al., 2007). However, the relationships between the LPFC and LOTC are still controversial. It is widely assumed that their relationship is hierarchical, and that the LOTC functions at a relatively lower level (Cattaneo, Sandrini, & Schwarzbach, 2010; Hamilton & Grafton, 2008). On the other hand, more recent neuroimaging studies have shown that the LOTC, rather than frontal regions, is involved in representing actions at the abstract level (Oosterhof, Tipper, & Downing, 2013; Wurm & Lingnau, 2015), challenging the conventional view. The relative contributions of these regions to the integration of signals required to detect both perfect and social contingencies remain unknown.

In the present study, we conducted a functional MRI experiment involving healthy adults to determine which brain regions are involved in the integration of signals associated with the relationships between self-produced and subsequently observed actions. The participants performed specific finger movements with the right hand, following which they observed various actions. We manipulated three factors: action kinematics (i.e., categories of finger actions), body identity, and