



Temporal dynamics of action perception: Differences on ERP evoked by object-related and non-object-related actions



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ABSTRACT

While neuropsychological dissociations suggest that distinct processes are involved in execution or perception of transitive (object-related) and intransitive (non-object-related) actions, the few neuroimaging studies that directly contrasted the brain activations underlying transitive and intransitive gesture perception failed to find substantial differences between the two action types. However, the distinction could be visible on brain activity timing within the fronto-parietal network. In this study, we used Event-Related Potential (ERP) method to assess the temporal dynamics of object-related and non-object-related action processing. Although both meaningful, only object-related actions involve object motor features. Accordingly, perception of the two action types would show distinct neural correlates. Participants were presented with four movie types (ORA, Object-Related Action, NORA: Non-Object-Related Action and 2 control movies) and were instructed to perform tasks that required explicit or implicit action recognition (specific action recognition or color change detection). Movies were presented as Point-Light Display (PLD) and thus provided only information about gesture kinematics regardless of action type. ERP were computed during movie visual perception and analyzed as a function of movie type and task. The main result revealed a difference between ORA and NORA on the amplitude of the P3a component in the fronto-parietal region. The difference observed around 250 ms after movie onset do not likely origin from variation in low-level visual features or attention resource allocation. Instead, we suggest that it reflects incidental recruitment of object attributes during object-related action perception. The exact nature of these attributes is discussed.

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1. Introduction

Several influential models of gesture production suggest that distinct cognitive mechanisms are devoted to the execution of different gesture types. Based on the observation of apraxic patients, such models typically propose two distinct routes for action, a semantic route and a non-semantic route (Buxbaum, 2001; Cubelli, Marchetti, Boscolo, & Della Sala, 2000; Gonzalez, Ochipa, & Heilman, 1991). The two routes would be differentially involved in the production of meaningless, transitive, and intransitive gestures. While imitation of meaningless gestures can only rely on the direct, non-semantic route for action, execution of both transitive (i.e. object-related) and intransitive (i.e. non-object-related) gestures can tap onto the semantic or

non-semantic route. In other words, executing intransitive actions as well as pantomimes of object use may involve semantic representations. However, it is still unclear whether transitive and intransitive gestures rely on distinct cognitive and neural mechanisms.

Distinction between production of transitive and intransitive gestures has been first documented in the neuropsychological literature. Patients with strongly impaired transitive gesture production and relatively preserved intransitive gesture execution have been reported many times following left hemisphere lesions (Dumont, Ska, & Schiavetto, 1999; Foundas et al., 1995; Haaland, Harrington, & Knight, 2000; Rapcsak, Ochipa, Beeson, & Rubens, 1993; Roy, Square-Storer, Hogg, & Adams, 1991). Based on these observations, it has been suggested that transitive and intransitive gesture execution rely on distinct cognitive networks. However, transitive gestures could be simply more difficult to perform than intransitive gestures. Several behavioral results are consistent with this alternative interpretation. Using more refined measures of gesture production accuracy, Carmo and Rumiati (2009) revealed

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that healthy participants imitated intransitive gestures better than transitive gestures (see also Mozaz, Rothi, Anderson, Crucian, & Heilman, 2002, for similar results). Thus, differences in gesture execution complexity could account for the greater deficits in transitive gesture production frequently reported in apraxic patients.

In this context, neuroimaging studies have tried to identify the neural substrates that would be specific to transitive action planning and execution (Bohlhalter et al., 2009; Culham, 2004; Fridman et al., 2006; Johnson-frey, Newman-norlund, & Grafton, 2005; Króliczak & Frey, 2009). Although both gesture types recruit a left-lateralized fronto-parietal network (but see Bohlhalter et al., 2008 for a right hemispheric dominance for intransitive gestures), some areas of this network have been shown to be more active during preparation and/or execution of transitive compared to intransitive actions (Buxbaum, Kyle, Grossman, & Coslett, 2007; Culham et al., 2003; Fridman et al., 2006; Haaland et al., 2000; Króliczak & Frey, 2009; Wheaton & Hallett, 2007). As suggested by Króliczak and co-workers in their interpretation (Króliczak & Frey, 2009), the differences observed may also depend on movement complexity since sensory-motor cortex activity and movement complexity are closely linked (Gut et al., 2007). Thus, findings from neuroimaging studies corroborate neuropsychological observations and suggest that the stronger fronto-parietal involvement observed during production of transitive compared to intransitive gestures is probably caused by greater difficulty of transitive gesture execution.

Recently, the pattern of apraxic deficits presented by an autistic child re-fueled the debate on the transitive–intransitive gesture distinction. Ham, Bartolo, Corley, Swanson and Rajendran (2010) reported the case of JK, who exhibited a selective impairment in producing intransitive gestures with normal scores in transitive gesture production. The existence of a double dissociation between the deficits presented by this child and the impairments of apraxic patients showing the opposite pattern suggests that the difference between transitive and intransitive gesture execution goes beyond difficulty.

In the present study, we aimed at investigating the neural correlates of transitive (object-related) and intransitive (non-object-related) action processing in perceptual tasks. We used perceptual tasks for two reasons. First, neuroimaging studies using production tasks lack appropriate baseline conditions for transitive and intransitive gesture comparison (Króliczak & Frey, 2009). Since gesture complexity is not matched between action types, it is tricky to draw conclusions about the specific neural substrates of object-related and non-object-related actions from production data. This limit is less difficult to overcome in perception. Accordingly, we designed perceptual control stimuli that were equivalent to the perceived transitive and intransitive actions in term of visual complexity. Second, in order to keep transitive and intransitive gestures equivalent, objects could not be presented. Moreover, we wanted to avoid pantomime tasks, since there is evidence of partially distinct neural circuits for real and pantomimed gesture execution (Króliczak, Cavina-Pratesi, Goodman, & Culham, 2007; Senkfor, 2008). Thus, the use of a perceptual paradigm allowed the assessment of object-related actions without involving objects or pantomimes.

On one hand, the two routes of action models (Buxbaum, 2001; Cubelli et al., 2000; Gonzalez Rothi et al., 1991) suggest that both object-related and non-object-related actions could involve some kind of semantic representations. On the other hand, it has been argued that in many situations, object-related actions require accessing both action and object representations (Buxbaum, 2001; Frey, 2007). This characteristic can obviously not apply to non-object-related actions, suggesting that additional semantic processes are involved in visual perception of object-related actions. Thus, perception of object-related actions, but not non-object-related actions, would involve the recruitment of object knowledge and in particular object motor features (Buxbaum et al., 2007; Chao & Martin, 2000; Martin, 2007). Based on

this idea and on the double dissociation observed in production (Dumont et al., 1999; Foundas et al., 1999; Haaland et al., 2000; Ham et al., 2010; Rapcsak et al., 1993; Roy et al., 1991), differences in cerebral activity during observation and recognition of object-related and non-object-related actions should be expected. In perceptual tasks, neuroanatomical and neuroimaging studies that directly compared object-related and non-object-related actions are even more limited (Agnew, Wise, & Leech, 2012; Pazzaglia, Smania, Corato, & Aglioti, 2008; Villarreal et al., 2008). Villarreal et al. (2008) have reported some differences in the inferior frontal gyrus (IFG) between the action types. However, they have been related to extra-processing demands for non-object-related gesture perception, probably because of the symbolic nature of the gestures presented (e.g., stop, salute, hitch hike, crazy, victory). Recently, Agnew et al. (2012) showed different fMRI responses in frontal and parietal cortices during observation of object-related compared to meaningless non-object-related actions, but results could be due to the use of meaningless action in the non-related action condition. Indeed, fronto-parietal areas may be more strongly recruited when action processing follows the semantic route, regardless of the type of semantic representation involved. Taken together, patient and fMRI studies have not provided a coherent pattern of data in support of a clear distinction between object-related and non-object-related gesture processing during action production or perception.

One possible reason for the inconsistencies reported may be that the distinction between object-related and non-object-related actions is relatively fine-grained and more visible on the timing of brain activity within the fronto-parietal network. Accordingly, fMRI paradigms would not be best suited to investigate this issue. Thus, we used EEG measurement and particularly Event-Related Potential method (ERP) to assess the temporal dynamics of object-related and non-object-related action processing during perceptual tasks. With EEG, we could determine the specific moment in processing when differences between action types emerged. It was thus possible to discriminate between effects related to visual complexity occurring at early processing stages and semantic effects occurring at later processing stages. Although the neural correlates of action observation have been importantly studied using EEG techniques (e.g. Silas, Levy, Nielsen, Slade, & Holmes, 2010 using whole-body movements, Perry & Bentin, 2009 using hand grasps or Urgen, Plank, Ishiguro, Poizner, & Saygin, 2013 for comparison between human and non-human motion), to the best of our knowledge no EEG paradigm has explicitly contrasted object-related and non-object-related actions before.

In light of previous studies, it was critical for our EEG paradigm to control for differences in stimulus complexity between the two action types. Thus, we used point-light display (PLD) stimuli (Johansson, 1973) in order to control for physical differences between stimuli. Indeed, baseline control PLD stimuli were created for each action type, in which the general movement characteristics (duration, number of points and kinematic of points) were equal to the original action but movement information was meaningless. Moreover, PLD stimuli provided biological movement information only – without giving any object visual information in the case of object-related action – and minimized context effects. Thus, we are able to test the distinction between temporal dynamics of object-related and non-object-related action processing with strictly equivalent stimuli, while controlling for potential differences in stimulus complexity.

Although time-frequency analysis, and in particular mu rhythm modulation, has been successfully used to highlight motor system involvement during observation of PLD of biological movements (Perry & Bentin, 2011; Perry, Troje, & Bentin, 2010), mu rhythm modulation would not be expected to be sensitive to semantic differences during action observation. Since the objective of the present study was to distinguish between the semantic processes

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