



## Research report

# Temporal dynamics of neural activity underlying unconscious processing of manipulable objects

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## ABSTRACT

The primate visual system is assumed to comprise two main pathways: a ventral pathway for shape and color perception and a dorsal pathway for spatial processing and visuomotor control. Previous studies consistently reported strong activation in the dorsal pathway (especially in the inferior parietal region) induced by manipulable object images such as tools. However, it is controversial whether the dorsal pathway retains this preferential activity to tool images under unconscious perception. In the present study, we used magnetoencephalography (MEG) and investigated spatio-temporal dynamics of neural responses to visible and invisible tool images. A presentation of visible tool images elicited a strong neural response over the parietal regions in the left hemisphere peaking at 400 msec. This response unique to the processing of tool information in the left parietal regions was still observed when conscious perception of tool images was inhibited by interocular suppression. Furthermore, analyses of neural oscillation signals revealed a suppression of  $\mu$  rhythm (8–13 Hz), a neural index of movement execution or imagery, induced by both visible and invisible tools. Those results indicated that the neural circuit to process the tool information was preserved under unconscious perception, highlighting an implicit aspect of the dorsal pathway.

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## 1. Introduction

Many studies have provided considerable evidence for the “unconscious” processing of sensory stimuli in the brain (Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Fang & He, 2005; Sterzer, Jalkanen, & Rees, 2009). To elucidate differences in neural mechanisms between conscious and unconscious sensory processing is one of the important themes in neuroscience and psychology (Block, 2005; Crick & Koch, 2003; Tönoni & Edelman, 1998).

Previous studies have approached this issue mainly using visual stimuli, partly because of a number of psychophysical techniques to make visual stimuli invisible (Dehaene et al., 2001; Hesselmann & Malach, 2011; Jiang & He, 2006; Sterzer et al., 2009). In the primate brain, there are two major pathways that receive and process visual information from the retina; the ventral (what) and dorsal (where or how) pathways (Ungerleider & Mishkin, 1982). The ventral pathway projects from the primary visual cortex (V1) through the ventral occipital structures to anterior temporal cortex. This pathway is

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dedicated to processing object identities (Fujita, Tanaka, Ito, & Cheng, 1992). On the other hand, spatial and visuomotor analyses to grasp and manipulate objects are performed by the dorsal pathway that projects from V1 through the dorsal occipital to posterior parietal cortices (Creem-Regehr & Lee, 2005; Milner, 2012; Proverbio, Adorni, & D'Aniello, 2011).

It was suggested that those two pathways have different categories of preferred stimuli. The most well-known stimulus that effectively activates the ventral pathway is faces. Electrophysiological studies using monkeys (Perrett et al., 1985; Tsao, Freiwald, Tootell, & Livingstone, 2006) reported that some neurons in the inferior temporal cortex show a particularly strong response to faces than other categories of objects (face-selective neurons). Accordingly, recent studies of fMRI on human subjects (Kanwisher, McDermott, & Chun, 1997) found brain regions specialized for the processing of face stimuli, such as the occipital face area (OFA) and the fusiform face area (FFA). Another line of studies (Anaki, Zion-Golumbic, & Bentin, 2007; Eimer, 2000; Itier & Taylor, 2004; McCarthy, Puce, Belger, & Allison, 1999; Miki, Watanabe, Honda, Nakamura, & Kakigi, 2007; Watanabe, Miki, & Kakigi, 2005) using electroencephalography (EEG) and magnetoencephalography (MEG) also reported neural responses from the occipito-temporal regions to face images (face selective N170/M170 in EEG/MEG). Those strong activities for specific categories of objects, however, were limited to visible images consciously perceived. When the stimuli were presented unconsciously, this lack of visual awareness to the stimuli substantially suppressed neural responses in the ventral regions (Lin & He, 2009). For example, Pasley et al. used interocular suppression, a psychophysical technique that renders visual stimuli invisible, and reported a near-complete inhibition of neural activities in the inferior temporal cortex to face stimuli unconsciously perceived (Pasley, Mayes, & Schultz, 2004). Although some studies indicated a possibility of residual activities to invisible face stimuli (Jiang & He, 2006; Sterzer et al., 2009; Suzuki & Noguchi, 2013), those studies overall show a substantial change of neural activities in the ventral regions depending on whether the stimuli are perceived consciously or unconsciously.

In contrast to the ventral pathway, it remains to be elucidated how the lack of conscious percept affects neural activities in the dorsal pathway. Although a classical theory proposed a dichotomy between “what” and “where” (or “how”) streams (Ungerleider & Mishkin, 1982), more recent studies provided evidence for further anatomical and functional distinctions within the dorsal pathway (Rizzolatti, Luppino, & Matelli, 1998). In a well-known (two-systems) model, the dorsal stream was divided into two sub-pathways; the dorso-dorsal pathway for an online control of action and the ventro-dorsal pathway for skilled action and action recognition (Binkofski & Buxbaum, 2012; Buxbaum & Kalenine, 2010; Rizzolatti & Matelli, 2003). The dorso-dorsal pathway, typically running from the visual area 6 (V6) and the superior parietal lobe (SPL) to the dorsal premotor cortex, processes structural information (size and shape, etc.) of visual stimuli at which actions are directed. This circuit is mainly concerned with the online control and spatio-motor transformations for reaching and grasping. On the other hand, the ventro-dorsal pathway, projecting from the medial superior temporal area

(MST) into inferior parietal lobe (IPL), is related to long-term storage of the skilled actions with familiar objects. This circuit is known to play a major role in tool use.

Consistent with the two-systems model in the dorsal pathway, previous studies showed that viewing tools enhanced neural responses in the inferior parietal regions (Bach, Peelen, & Tipper, 2010; Frey, 2007). Additional activities were also observed in motor-related regions including the premotor and somatosensory areas (Chao & Martin, 2000; Grafton, Fadiga, Arbib, & Rizzolatti, 1997; Grezes & Decety, 2002; Kellenbach, Brett, & Patterson, 2003), even when no overt actions were required in a task (Creem-Regehr & Lee, 2005). Those activities in the inferior parietal and motor-related regions were especially strong in the left hemisphere (Chao & Martin, 2000; Creem-Regehr & Lee, 2005; Grafton et al., 1997; Grezes & Decety, 2002; Kellenbach et al., 2003), which is also a hallmark of the dorso-ventral pathway (Binkofski & Buxbaum, 2012). Interestingly, a previous fMRI study reported that those activities in the parietal regions were mostly unchanged even when tool images were made invisible by an interocular suppression (Fang & He, 2005). This visibility-invariant property in the dorsal pathway is consistent with a case report of patient D.F. who had a severe bilateral damage in the occipito-temporal areas (Goodale & Milner, 1992; Goodale, Milner, Jakobson, & Carey, 1991). Despite her inability of discriminating simple geometric shapes, she could use information from objects (e.g., tools) unconsciously to guide her hand movements. Those findings suggest that neural processing in the dorsal pathway is performed implicitly and thus is not available to conscious awareness (Milner, 2012). However, another recent study of fMRI provided the data inconsistent with this view (Hesselmann & Malach, 2011). Using continuous flash suppression (CFS) (Tsuchiya & Koch, 2005), they showed that an inhibition of conscious perception of tool images substantially reduced neural responses in the V1 and dorsal pathway. It is therefore controversial whether the dorsal pathway retains significant neural responses to invisible tool images.

In the present study, we combined CFS with MEG measurements and examined a role of the dorsal pathway in the processing of invisible tools. There are two advantages of using MEG. First, we could directly measure neural activities related to face and tool perception with a fine temporal resolution. As described above, the brain responses to tool images are characterized by a flow of neural activities from the visual area to the parieto-frontal regions via the dorsal (ventro-dorsal) pathway. Therefore, we investigated whether neural activities in this elemental circuit for tool processing are observed in unconscious as well as conscious perception. Second, the use of MEG enables us to analyze oscillation signals in neural activities. A previous study (Proverbio, 2012) reported that conscious perception of tool images (without motor responses) induced a neural desynchronization in upper  $\mu$  frequency band (10–12 Hz) over centro-parietal sites. If this phenomenon is also observed under unconscious condition in the present study, those results would provide additional evidence for a preservation of the neural circuit to process manipulable objects in unconscious perception.

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