

THE NEURAL SUBSTRATE OF THE IDEOMOTOR PRINCIPLE REVISITED: EVIDENCE FOR ASYMMETRIES IN ACTION-EFFECT LEARNING

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Abstract—Ideomotor theory holds that the perception or anticipatory imagination of action effects activates motor tendencies toward the action that is known to produce these effects, herein referred to as *ideomotor response activation* (IRA). IRA presupposes that the agent has previously learned which action produces which effects, and that this learning process has created *bidirectional* associations between the sensory effect codes and the motor codes producing the sensory effects. Here, we refer to this process as *ideomotor learning*. In the presented fMRI study, we adopted a standard two-phase ideomotor learning paradigm; a mixed between/within-subjects design allowed us to assess the neural substrate of both, IRA and ideomotor learning. We replicated earlier findings of a hand asymmetry in ideomotor processing with significantly stronger IRA by left-hand than right-hand action effects. Crucially, we traced this effect back to more pronounced associative learning for action-contingent effects of the left hand compared with effects of the right hand. In this context, our findings point to the caudate nucleus and the angular gyrus as central structures of the neural network underlying ideomotor learning. © 2012 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: motor control, executive functions, associative learning, caudate nucleus, fMRI.

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Abbreviations: BOLD, blood oxygen level dependent; FPC, frontopolar cortex; IRA, ideomotor response activation; SMA, supplementary motor area; TPJ, temporo-parietal junction.

INTRODUCTION

The term *ideo-motor* was coined in the middle of the 19th century, at a time when Europe was captivated by alleged paranormal phenomena ascribed to transcendent powers like table turning or magical pendulums (Tischner, 1929). Carpenter (1882) tried to explain these phenomena by referring to unwilled and unconscious motor excitation elicited by the anticipatory imagination (“idea”) of a specific effect. For instance, thinking of a swinging or rotating pendulum may unconsciously trigger tiny muscle activation in the fingers which hold the pendulum and thereby produce the imagined motion: the “*ideomotor reflex*”.

Since then, the principle of triggering motor actions by effect anticipations has been embedded into a broad conceptual framework. Today, it is no longer seen as an involuntary reflex, bound to conditions of reduced will and expectant attention, but rather as a ubiquitous mechanism in voluntary action control – a truly executive function (James, 1890; see also Hommel et al., 2001; Pfister and Janczyk, 2012; Shin et al., 2010). In the following, we will refer to the mechanisms that relay sensory anticipations to motor centers as *ideomotor response activation* (IRA). This process relies on bidirectional associations between motor codes and sensory effect codes that have to be learned (Elsner and Hommel, 2001; Hoffmann et al., 2009). Once such action-effect associations have been acquired, activating a sensory effect code will automatically spread activation to the associated motor codes.

To put it in a broader theoretical framework, ideomotor assumptions can be related to general models of action control or limb praxis. One of the most influential theories of limb praxis was put forward by Rothi et al. (1991, 1997), a two-route model which distinguishes between the performances of familiar or meaningful movements on the one hand and unfamiliar or meaningless movements on the other. The former and only these would recruit on the so-called “output praxicon”, a specialized long-term mnemonic structure which stores visuo-kinaesthetic attributes of movements, i.e. performance-related sensational or perceptual codes, which for movement execution are directly transcoded into motor programs. Entries of the output praxicon, in turn, get activated by more “passive” perceptual representations of physical characteristics (amplitude, spatial orientation, etc.) of actions, posited to be stored in another neurocognitive structure, the

so-called “input praxicon”. According to the theory, the input praxicon allows to identify familiar actions of the agent’s repertoire, whereas the output praxicon supplies the motor implementation of actions at the innervatory pattern stage. Importantly, the outlined executive mechanism avoids the costs incurring for unfamiliar actions which require computing all the parameters needed to implement the spatial and temporal characteristics of intended movements (cf. Rothi and Heilman, 1996). There is an obvious similarity between the theoretically posited functionalities of output praxicon content on the one hand and learned action effects on the other, which are both assumed to be automatically transcoded into motor programs.

Similarly, ideomotor learning can be conceptualized as acquisition of a so-called *inverse internal model* (Wolpert and Kawato, 1998) which is a feedforward controller of motor action in which the output is identical to the input information. Basically, skillful coordinated limb movements arguably cannot be executed solely under feedback control, because feedback loops are generally slow and have small gains. Therefore, the brain needs to acquire an inverse dynamics model of intended action through motor learning, after which motor control can be executed in a pure feedforward manner (cf. Kawato, 1999; Wolpert and Ghahramani, 2000).

Whereas first neurophysiological studies have targeted the process of IRA (Elsner et al., 2002; Melcher et al., 2008; Kühn et al., 2011), the neural mechanisms underlying the preceding *ideomotor learning* are virtually unknown. Accordingly, the present study investigated the neural mechanisms underlying ideomotor learning and their relation to subsequent IRA.

To this end, we adopted a two-phase design that was previously used to assess the neurophysiological basis of IRAs (Melcher et al., 2008; cf. also Elsner and Hommel, 2001; Pfister et al., 2011). In an *acquisition phase*, participants performed key press actions to produce arbitrary action effects which in different subject groups were either contingent or non-contingent with the selected response. Thus, both groups had overall comparable sensory and motor activities but a different potential to exhibit ideomotor learning. In the subsequent *test phase*, participants of the contingency group were probed for IRA. Effect stimuli (i.e. stimuli which were presented as action effects during the acquisition phase) were now presented together with an imperative target stimulus¹, which prompted participants either to freely choose a response or to withhold responding (Fig. 1). No-go trials of the latter kind allow defining the neural correlates of the perception of learned action effects independent of proper motor activation: *the pure neural substrate of IRA* (cf. Elsner et al., 2002; Melcher et al., 2008). The presence of go trials on the other hand increases the response readiness of subjects

and thus assumably promotes effects of IRA during no-go trials².

As outlined above, previous neurophysiological studies only investigated IRA (in more technical terms: the test phase) and neglected the underlying learning process (the acquisition phase). In these studies, IRA was mirrored in activity of the supplementary motor area (SMA) and the hippocampal system (Elsner et al., 2002; Melcher et al., 2008). The major goal of the present study was to investigate the learning process enabling such response activation effects. Interestingly, response activation effects in previous studies were entirely driven by structures associated with declarative memory such as the hippocampus or the parahippocampal gyrus. This medial temporal memory system is typically distinguished from a second, ‘habit learning system’ in the basal ganglia, i.e. comprising the putamen and caudate nucleus (e.g., Knowlton et al., 1996; Packard and Knowlton, 2002). Given that this second memory system was repeatedly associated with motor learning (see Seger, 2006, for a review), we expected ideomotor learning to draw on this system in addition to the medial temporal system (Tricomi et al., 2004).

Moreover, previous studies suggest that memory-based sensorimotor transformation or integration – i.e. output praxicon function (see above) – is represented in temporo-parietal regions. In this context, Peigneux et al. (2004), for instance, emphasized the contribution of the superior temporal cortex (superior temporal sulcus) in the sensory processing of action-related stimuli or proper motions. Rumiati et al. (2005) report a left-hemispherical pattern of increased activity comprising the inferior temporal gyrus and angular gyrus specifically in response to familiar actions, while Grèzes et al. (1999) related the inferior parietal cortex and the frontopolar cortex (FPC) to the acquisition of familiar actions during action observation (i.e. during visuomotor learning). Based on the outlined findings, ideomotor learning as a special instance of sensorimotor integration can be reasonably expected to rely on temporo-parietal regions in addition to genuine memory- or learning-related structures of the basal ganglia and the hippocampal system.

Furthermore, it is important to note that the described network for IRA found in previous studies only emerged for the left-hand but not for right-hand action-effects, indicating a fundamental asymmetry of ideomotor processes (cf. Melcher et al., 2008). Because the latter

¹ In the present work, we use the term “target” or “target stimulus” to denote task-relevant stimuli which one, according to the task-rules, has to recognize for response selection. These stimuli can be distinguished from non-targets, which have no direct relevance for task performance.

² In contrast to behavioral studies on ideomotor response activation (Dutzi and Hommel, 2009; Elsner and Hommel, 2001; Pfister et al., 2011; Hoffmann et al. 2009), the present study and the Melcher et al. (2008) study did not present effect stimuli as targets (i.e. task-relevant imperative stimuli) but only as additional stimuli accompanying the target. This procedure enables a within-subjects assessment of ideomotor response activations independent of proper motor activation by neurophysiological techniques (e.g. fMRI). This advantage, however, comes at the price of diminished behavioral effects. Accordingly, the present study did not find specific behavioral “ideomotor” effects for go trials at the regular statistical threshold – nor did Melcher et al. (2008) – which we expected and accepted already in the study planning. In the main manuscript we will thus focus exclusively on the neurophysiological data. A presentation of the behavioral data and related explications are given in Appendix.

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