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Pictures of you: Dot stimuli cause motor contagion in presence of a still human form



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ABSTRACT

In this study, we investigate which visual cues induce participants to encode a non-human motion stimulus in their motor system. Participants performed reach-to-grasp actions to a target after observing a dot moving in a direct or higher-arching path across a screen. Dot motion occurred in the presence of a meaningless (scrambled human model) stimulus, a still human model, or a human model performing a direct or exaggeratedly curved reach to a target. Our results show that observing the dot displacement causes motor contagion (changes in the height of the observer's hand trajectory) when a human form was visually present in the background (either moving or still). No contagion was evident, however, when this human context was absent (i.e., human image scrambled and not identifiable). This indicates that visual cues suggestive of human agency can determine whether or not moving stimuli are encoded in the motor system.

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1. Introduction

It has long been established that observing others' actions affects how we ourselves move. In 1890, William James described the ideomotor principle: the mere thought of an action (whether generated internally or by observing another person's) translates into action execution (James, 1890; see also Carpenter, 1852, in Shin, Proctor, & Capaldi, 2010). The discovery of mirror neurons in macaques (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996) and corresponding systems in human cortex (Rizzolatti et al., 1996) provided a candidate neural substrate for this process (see Rizzolatti & Craighero, 2004), and sparked a resurgence of interest in this phenomenon.

At least two patterns of behavioural evidence align with the ideomotor principle. First, initiating an action is slower after observing an incompatible action compared with a compatible one (Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschläger, & Prinz, 2000). This is often referred to as ideomotor priming (Brass et al., 2001; also motor priming, Bertenthal, Longo, & Kosobud, 2006; visuomotor priming, Craighero, Fadiga, Umiltà, & Rizzolatti, 1996; automatic imitation, Longo, Kosobud, & Bertenthal, 2008; Press, Bird, Walsh, & Heyes, 2008). For example, an early paradigm involved participants executing finger lifting or tapping movements while observing films or image sequences of the same (Brass et al., 2001). Initiation of an index finger lift, for example, was slowed following observation of an index finger tap (Brass et al., 2001). Other commonly used action pairs include lifting the index versus middle finger (for example, Brass et al., 2000) or closing versus opening the hand from a neutral position (for example, Press et al., 2008). In both paradigms, participants' responses are initiated faster when making congruent compared with incongruent movements (Brass et al., 2000, 2001; Press et al., 2008).

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Ideomotor priming effects show that action observation modulates action planning and initiation, but do not clarify whether the executed movement itself is altered. The second pattern of behavioural effects deals with this question. The results of several experiments show systematic, involuntary alterations in motor output parameters of the observer that correspond to the specific kinematic parameters of the model's action (Griffiths & Tipper, 2009, 2012; Hardwick & Edwards, 2011; Kilner, Paulignan, & Blakemore, 2003; Sparks, Douglas, & Kritikos, 2016), which we term 'motor contagion'. In one such paradigm, participants are instructed to execute direct, natural reach-to-grasp actions toward a target object (Griffiths & Tipper, 2009; Hardwick & Edwards, 2011). Participants observe a model execute a reach with either a direct, natural trajectory or an exaggerated trajectory that attains much greater wrist height, and immediately afterwards execute a direct or exaggerated reach. Compared with viewing direct trajectories, viewing exaggerated trajectories caused participants' maximum wrist height to increase. Additionally, Bisio, Stucchi, Jacono, Fadiga, and Pozzo (2010) report a similar transfer of observed velocity kinematics to executed kinematics. Together these findings suggest that the model's motor output 'resonates' with the observer's motor repertoire and subsequently alters the observer's unfolding motor output (Griffiths & Tipper, 2009; Hardwick & Edwards, 2011; Kilner et al., 2003; Sparks et al., 2016).

Modern formulations of ideomotor theory (e.g., Common Coding theory, Aschersleben & Prinz, 1995; Theory of Event Coding, Hommel, 1998, 2009; Hommel, Müsseler, Aschersleben, & Prinz, 2001) continue to account for these findings by proposing an overlap in the representations for observed and planned actions. The Theory of Event Coding describes this common format in terms of feature codes bound within event files (Hommel, 1998, 2004; and see Treisman & Gelade, 1980). Observing or executing an action within a given context generates an event file, consisting of features that are related to the action and its perceptual context and that are bound together. Crucially, there is no distinction between observed and planned actions. Visual features from observed actions therefore can reactivate motor components of those actions.

Observing non-human motion also affects our motor output (Gowen, Bolton, & Poliakoff, 2016; Gowen, Bradshaw, Gaplin, Lawrence, & Poliakoff, 2010; Kilner, Hamilton, & Blakemore, 2007). For example, observing an abstract object (e.g., a rectangle) displaced in a direction incompatible with the direction the observer must execute can slow the observer's movement initiation in a manner analogous to ideomotor priming (Gowen et al., 2016) or interfere with movement trajectory in a manner analogous to motor contagion (Kilner, Hamilton et al., 2007). In light of this, there is growing interest in what distinguishes encoding of human-generated motion stimuli from non-human motion stimuli, and what governs how the system deals with moving stimuli of ambiguous origin (Gowen & Poliakoff, 2012).

Strong evidence has emerged that the observer's beliefs about agency play a key role in determining how moving stimuli are processed (for review, see Gowen & Poliakoff, 2012; see also Cross, Ramsey, Liepelt, Prinz, & de C. Hamilton, 2016; Heyes, 2011). Stanley, Gowen, and Miall (2007) had participants view a dot moving while themselves executing compatible or incompatible arm movements relative to its trajectory. When participants were told that the dot represented pre-recorded human movement, motor contagion effects emerged. In contrast, no motor contagion was evident when participants were told the dot's movement was computer-generated. Importantly, there were no differences in the stimulus parameters, which rules out any explanation based on bottom-up stimulus-driven factors. This suggests that moving stimuli are more likely to affect motor output when the observer believes they are human-generated.

Belief about agency not only determine *if* a movement stimulus modifies executed action, it can determine the *how* the executed action is modified. Gowen et al. (2016) displayed moving shape stimuli and in a first block gave participants no information regarding their origin (human or otherwise). The stimuli evoked spatial compatibility effects in initiation time in this condition. In a subsequent block, they instructed participants that the shapes represented human fingers moving with the hand positioned such that ideomotor priming effects would occur in the reverse direction to the initial spatial compatibility effects. This manipulation did indeed reverse the response compatibility effect. These finding suggests that beliefs about agency can induce a qualitative change in the manner a stimulus is encoded to such an extent that pure spatial compatibility effects are completely overridden.

As reviewed above, there is clear evidence that semantic information (implemented via verbal instructions) relating to agency has a strong impact on encoding of moving stimuli with ambiguous origins. It is less clear how the system determines whether or not to attribute agency in the absence of such semantic input. For example, in Kilner, Hamilton et al.'s (2007) study where ball motion elicited motor contagion, there was no explicit semantic instruction regarding the origin of the ball's motion. It is possible that participants tended to believe the ball movement was agentic and therefore motor contagion emerged in their own movements. This would reconcile Kilner et al.'s results with the lack of motor contagion Stanley et al. (2007) observed using similar stimuli when they explicitly instructed participants that the movement was non-agentic. This highlights an important point: Top-down factors, especially beliefs about agency, are likely to play even when they are not explicitly manipulated or controlled in an experiment via verbal or written instruction.

There is converging evidence that human perception incorporates Bayesian probabilistic reasoning (for example, Kersten, Mamassian, & Yuille, 2004; Kilner, Friston, & Frith, 2007). We suggest that probabilistic reasoning applies when determining whether a movement stimulus is agentic versus non-agentic. Agency is ascribed to a movement based on the evidence provided by available cues, whether implicitly or explicitly. These cues may be perceptual (e.g., human form and biological velocity profile) and/or semantic (e.g., spoken or written information about the movement's origin). Humans are capable of controlling objects that do not resemble the human form (e.g., a tool or a moving mouse cursor) and of wearing clothing that may obscure biological motion cues. Probabilistic reasoning for ascribing agency to movements may be very flexible if it

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