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Recruitment of the motor system in the perception of handwritten and typed characters

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Abstract

Many different functional roles have been ascribed to the motor system due to its prevalent recruitment in perceptual and cognitive tasks other than motor production. We discuss findings that suggest the motor system might take on multiple roles that vary with context and the brain networks involved. Using single-pulse TMS, we measured the corticospinal excitability of the FDI muscle in primary motor cortex as participants viewed words that were either typed or handwritten. We observed consistent facilitation of corticospinal excitability during reading of handwritten text. Although we observed facilitation in corticospinal excitability during the presentation of typed text, this effect decreased with repetitive presentations of stimuli. We suggest that the facilitation during presentation of typed words is a case of action simulation, and that the diminishing facilitation in the case of typed stimuli is representative of sensory prediction by the motor system. These findings suggest that we should consider multiple roles for motor recruitment during the observation of visual stimuli, taking context into consideration.

Keywords: Action observation, motor involvement in reading, sensorimotor prediction.

Introduction

The motor system is involved in a large number of cognitive and perceptual domains, including action observation, perception of object affordances, speech perception, language and metaphor, and social cognition. There are many theories aimed at explaining this widespread use of the motor system. We will introduce some of these theories here and work supporting each of them. Then we provide an alternative hypothesis: that there is no one particular role for the motor system in perception and cognition, but that it plays many roles decided, in part, by situational context.

Outside of its role in moving the body, the most common and widely posited role of the motor system is in observation-execution mapping. A network which includes several motor regions of the brain is responsible for mapping observed actions onto one's own motor system, which is said to underlie action understanding. The neurological underpinnings of this system rely on particular neurons in motor cortex, called mirror neurons, that fire during both observation and performance of a motor act in macaque monkeys and in humans. (Rizzolatti et al. 1988, di Pellegrino et al., 1992; Gallese et al., 1996; Mukamel et al., 2010). Umiltà et al. (2001) found that some subset of mirror neurons fire during the final part of an observed action, even if that final part of the action is occluded from view, suggesting that mirror neurons code the goal-related execution of an action. This also suggests that mirror neurons respond to action-related situations where determining the actor and situation involves more inference, suggesting a role in deeper understanding of action. Kohler and colleagues (2002), recording from single neurons in monkey premotor cortex, found that some of the same neurons that fire during observed action will also fire when monkeys are only hearing the auditory information from the action (i.e., the cracking of a peanut). Again, this involves inference to the presence of the actor without visual recognition.

Motor activation during action observation is also called motor resonance (Iacoboni, 1999), due to its time-dependent and effector-specific nature. It is said that the motor system of the observer "resonates" with that of the actor, allowing the observer to use their own body to understand the action being performed. Gangitano, Mottaghy, and Pascual-Leone (2001) applied transcranial magnetic stimulation (TMS) to record motor-evoked potentials (MEPs) from the first dorsal interosseus (FDI) muscle on the right hand during the observation of a cyclic hand movement. They found that at the time when the FDI muscle of the observed hand was most contracted, MEPs in the observer were highest, and when the muscle was least contracted, MEPs were lowest. Thus, the motor resonance occurring in the observer is timelocked with specific muscle activity in the observed agent.

A related theory of motor system involvement is that of overt action simulation (Barsalou, 2009; Gallese and Lakoff, 2005). This is related to the above mentioned position and not mutually exclusive, as observation-execution matching could involve low-level simulation of an actor. Simulation theories, however, posit explicit ongoing simulation underlying perceptual and cognitive processes as a sort of online enactment, particularly for understanding semantics of action language. In other words, linguistic phrases such as "the boy caught the ball" are understood by low level simulation of the action in the

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sentence. Numerous studies have shown that action language activates the motor system.

In an fMRI experiment, Hauk, Johnsrude, and Pulvermuller (2004) found that when participants read action words related to the arm, leg, or face, the corresponding regions of the motor somatotopy were active. Oliveri et al. (2004), using single pulse TMS, found that motor cortex activation increased for both action nouns and action verbs when compared to activation during non-action words. Candidi and colleagues (2010) found that verbs conjugated in the future tense induce higher corticospinal excitability than verbs conjugated in the past. Finally, Yang and Shu (2016) performed a meta-analysis on a large number of fMRI experiments where subjects were listening to literal action sentences, fictive motion sentences, metaphorical action sentences, and idioms, and found increased activation in motor regions during metaphorical action sentences. This activation is thought to contribute to understanding and mapping metaphors onto their concrete reference. Simulation theories are often associated with embodied cognition, proposing that we use our brains and bodies to ground conceptual and abstract content in sensorimotor systems.

The third theory we discuss is sensory prediction. In this case what is being coded for in the motor system is sensorimotor prediction, or continuous online prediction of the very next state of the stimulus. A predictive role for the motor system is suggested in Clark's (2015) theory of "embodied prediction", in which motor activation during action observation would entail prediction of the upcoming sensory signal based on the current sensory information. In this case, motor cortex would be active during the observation of a grasping action, because the observer's brain would be actively predicting the very next movement via motor regions. Thus, a predictive role can account for the findings from the action-observation network literature. Wilson and Knoblich (2005) outline a version of the perceptual prediction role of motor areas that uses what they call perceptual emulators. An emulator is a mental simulation that models the external world. The emulator continues updating the model online, and the output from this emulator can be compared to the actual state of the external world to verify that expectations are being met. Emulators running in the motor system would internalize a model of the biomechanics of the human body, allowing observers to model the movements of an observed agent as they unfold in time. Importantly, these emulators are running one step ahead of sensory input, predicting the upcoming external state before it happens and then comparing real to modeled state afterward.

If the motor system uses these emulators, it should also be able to model predictable sensory information that isn't human-made, such as rhythmic waves or the bouncing of a ball, by internalizing a model for the observed system. Supporting research comes from Schubotz (2007), whose work suggests that even observation of movements coming from non-animate entities recruits the motor system. In a number of fMRI experiments, they find that particular types of perceptual prediction tasks involving such things as pitch identification, spatial or object-related identification tasks activates premotor areas in a somatotopic way, similar to effector-related observation/execution tasks. For instance, object-related tasks recruited regions of premotor cortex that share activation in hand-related execution and observation tasks. As there isn't a common repertoire to humans and rolling waves, these findings could not be explained under the motor resonance account.

We propose that the role of the motor system varies depending on context. For instance, during the perception of action language, the motor system might serve to provide the motor component of covert simulation that occurs in the embodied processing of language. During the observation of very well practiced movements by an outside actor, the motor system may serve the purpose of driving motor resonance in the observer to quickly map the actions to the observer's body and understand the action. Finally, during perceptual processing of non-human movements, the motor system might serve to assist in perceptual processing by way of predictive emulator models.

One potential way of differentiating between prediction and simulation is by observing how the modulation of the motor system changes over repetitive viewing of stimuli. If the observer is simulating the observed action, then we should see a steady facilitation of MEPs across repetitions of a stimulus, indicating simulation at each occurrence. If motor system facilitation is due to predictive processes, however, might expect a different pattern of modulation. Because less error correction takes place as a stimulus becomes more predictable, we can predict that the neural populations underlying the predictive processes will be less active for more predictable sensory stimuli. Thus, we should see a decrease in corticospinal excitability over multiple repetitions of a stimulus, as it becomes more predictable and leads to lower error correction..

In this experiment we look at corticospinal excitability using single-pulse transcranial magnetic stimulation (TMS) during the perception of written language to examine the extent of motor involvement in a few variations of the stimuli. Subjects viewed videos of words being written out with a stylus and of words being typed letter by letter. Previous analyses in our lab have shown that observation of handwriting leads to motor simulation, while observation of typed words does not. We proposed that this is because while it is apparent that the handwritten text are human created, this is less apparent for text created on a keyboard. We repeat all stimuli four times over the course of the experiment. We predicted that MEPs in the handwritten stimuli trials would show an even facilitation across all presentations of the stimuli, because simulation should be consistent no matter how predictable it is. We hypothesized that the MEPs in the typed stimuli trials would show initial facilitation, which would lessen as the stimuli are repeated

and there is less prediction error. This would be expected because the first presentations of the stimuli, appearing letter by letter, should be difficult to predict, resulting in a large error in perceptual prediction. As stimuli are presented more often, perceptual prediction should become easier and less effort required on the part of error correction.

Methods

Participants:

Twenty-four right-handed normal participants (8 males, 16 females, mean age ~ 19.5) were recruited in this study through UC Merced's SONA research system. All participants passed a safety screen and gave written, informed consent. The experimental procedure was approved by the UC Merced Institutional Review Board. Participants received 2 research credits that can be used for credit in some undergraduate courses.

TMS and EMG recording:

Corticospinal excitability was measured by the amplitude of motor evoked potentials (MEPs) recorded using electromyography (EMG) on the first dorsal interosseus (FDI) muscle of the right hand. Two small adhesive electrodes (1cm^2) were placed over the belly of the recorded muscle and a ground electrode was placed over a bone on the participant's elbow. A bandpass filter (50 Hz1,000 Hz) was applied to the EMG signal, which was digitized at 1,000 Hz for offline analysis. MEPs were elicited by applying single-pulse TMS to the FDI region of the left motor cortex. Pulses were delivered using a Magstim Rapid² with an attached 70-mm figure-of-eight coil positioned over the optimal scalp location with the handle pointing backward at 45 degrees from the midline. The procedure was as follows. Subjects were fitted with a swim cap that was covered by a grid of dots placed 1 cm² apart. Optimal scalp position was determined by moving the coil by one centimeter intervals until the location eliciting the best MEPs was identified. This location was marked on the swim cap worn by the participant. Resting motor threshold was determined as the percent of machine output that produced 5 out of 10 MEPs of at least 50 µV peak-topeak amplitude. The stimulation intensity during the experiment was set to 120% of a participant's resting motor threshold. The coil was held steady at the optimal position throughout the experiment. Subjects were instructed to keep their head still and remain relaxed for the duration of the experiment.

Experimental paradigm:

The visual stimuli consisted of videos of either handwritten or typed words or nonwords appearing letter by letter at a variable typing speed averaging 3-4 letters per second. Words were chosen that did not relate to any actions or manipulable objects, to ensure that our measurement would not be influenced by the effects of semantic processing of

action. We also included 10 baseline trials, which consisted of a single black box for the same duration as the stimuli. We chose to randomize the baseline trials in with the rest of the trials so that the baseline measure would not be biased by a lack of attention that can occur when baseline measures are all recorded pre-experiment. Stimuli included ten linguistic stimuli, which appeared four times in each of the conditions. This resulted in 80 stimuli trials and 10 baseline trials, or a total of 90 trials. Eight seconds passed in between individual trials, and the total experiment length was approximately 12 minutes. We chose to apply stimulation two seconds into the ongoing video, so that as the stimuli were repeated, they were more highly predictable (by the presence of the first few letters) by the time stimulation occurred. Because TMS stimulation would occur two seconds into the video, we ensured that the typed stimuli would display one of the following letters at that time [N, H, U, M, J, I], so that if subjects were simulating the typing in proper typing position, FDI would be the simulated muscle.

The stimuli appeared on a computer screen in front of the participants. Participants were instructed to attend to the stimuli on the screen and were given notice when the experiment was one-third and two-thirds of the way finished to prevent loss of attention.

TMS pulses were delivered 2 seconds after video onset. The interval between trials was 8 seconds, to avoid any cumulative effects of single-pulse TMS. After the experiment, subjects were asked whether they were able to stay attentive during the length of the experiment. Participants who said they were not were excluded from analyses (5 subjects).
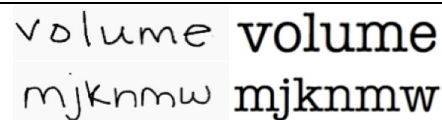

Figure 1: Examples of stimuli used in the experiment. Handwritten stimuli are on the left and typed stimuli on the right. In the experiment, participants saw the stimuli appear as a video as they were written or typed.

Results

The average raw MEP amplitude for handwritten stimuli was 1.126 mV, with a standard deviation of 1,303. The average for typed words was 1098 mV, with a standard deviation of 1.295. Because of the large variations between participants, raw MEP amplitude values were z-scored to allow inter-individual comparisons. The resulting z-scores indicate the distance (in standard deviations) that a particular MEP score is from the mean. Figure 2 shows the average z-score in each condition. The average z-score for handwritten stimuli was .1, while that for typed stimuli was -.06.

A two-way repeated-measures analysis of variance (ANOVA) was computed on the standardized MEPs to test

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for significant effects. The considered factors were condition (handwritten or typed) by order (nth time that a stimulus appeared). We observed a significant main effect for condition, with handwritten stimuli producing greater facilitation of MEP amplitude with respect to typed stimuli, $F(1,23) = 7.62$, $p < .01$. We also observed a significant interaction effect of condition by order of presentation, $F(3,184) = 3.77$, $p = .05$. In particular, there was a consistent facilitation in MEPs in the handwritten stimuli regardless of how many times the stimulus has been presented. In the typed stimulus condition, however, there was an initial facilitation in the MEP amplitude that decreased with each repetition of the stimuli. This pattern of results confirms our hypothesis of typed stimuli showing an initial facilitation of corticospinal excitability, followed by a decrease in that facilitation. This also confirms our hypothesis that the handwritten words would induce consistent facilitation of corticospinal excitability.

A linear regression of presentation number on baseline zscore was performed in order to evaluate whether the baseline MEPs changed with multiple presentations of the stimuli. The regression came out non-significant ($t = -1.1$, $p > .3$). This indicates that overall MEP amplitudes are not varying as a function of time or number of repetitions to stimuli.
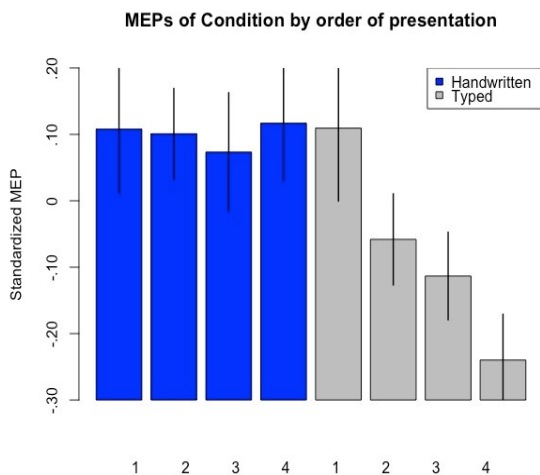

Figure 2: Standardized (Z-scored) MEP amplitudes for each condition. X-axis shows presentation number (nth time a stimulus was presented). Motor evoked potentials in the handwritten condition show consistent facilitation, while those in the typed condition show initial facilitation that decreases with presentation number.

Discussion

In this experiment we observed a differential pattern of motor facilitation dependent on word reading condition. In particular, the observation of actively handwritten words produced a persistent facilitation in MEP amplitudes. This is consistent with the action observation research, where subjects view actions produced by others over multiple trials and produce consistent MEP facilitation. When subjects are exposed to actively typed words, however, the pattern of MEP facilitation changes, with repetitive exposure to the stimulus resulting in a decrease in observed corticospinal excitability. In previous work, we hypothesized that typed stimuli might not show simulation because of two reasons. Either the act of typing has weak or no sensorimotor association, or the discrete nature of typed words does not invoke simulation the same as the continuous strokes of handwriting.

Evidently the motor system is doing something different from motor simulation during the observation of words that are actively typed. One potential hypothesis is that corticospinal excitability in the typed condition is influenced by attentiveness. As subjects are repeatedly exposed to words, they might lose interest and thus exhibit lower attention. We included in the experiment a baseline measure appearing randomly throughout, consisting of a solid black box that appears instead of the language stimuli. There were 10 baseline trials used. If corticospinal excitability was picking up on a measure of attention, we should see a predictable decreasing trend in MEP amplitudes across repetitions of the baseline trials as well. No such decreasing trend was observed over the repeated baseline trials. Though we cannot rule out the possibility entirely, this does suggest that there is something happening for the typed stimuli other than decreased attentiveness.

We suggest that the decrease in excitability across repetitions of stimuli is due to sensory prediction by the motor system. When the stimuli are less predictable (i.e., the first presentations), the sensory prediction error is large, resulting in higher motor activation. As the stimuli are repeated and become more predictable, the sensory prediction error becomes lower and we observe less corticospinal excitability in the motor system. This account is consistent with Schubotz's (2007) findings of motor activation during serial prediction tasks and Wilson and Knoblich's (2005) emulator account.

If our theoretical formulation is correct, this implies that the study of motor involvement in perception and cognition should take into account that the motor system is playing multiple processing roles that are network and contextdependent. The action observation based recruitment of the motor system is well established. Strong evidence suggests that this is due to motor resonance that is both effectorspecific and time-dependent. We contend that the role of motor cortex in action-observation is for low-level activation of one's own motor repertoire. Under our account, motor activation during perceptual processing of non-human-created stimuli, reported by Schubotz and colleagues, is not at odds with the resonance account of action observation. The particular information processing role of motor regions does not need to be identical across contexts. The functional network underlying action observation includes bilateral mid-temporal gyrus (MTG) and left

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inferior parietal lobule as well as left premotor cortex. (Gazzola, Aziz-Zadeh, & Keysers, 2006). Other brain regions active during figurative language include the left and right inferior frontal gyrus (IFG), bilateral medial frontal gyri (medFG), left temporal lobe, and amygdala. (Bohrn, Altmann, & Jacobs, 2012). The function of motor activation in each of these different networks can be defined by its connections and interactions, allowing a motor predictive system or motor simulation system when appropriate.

How would this region have multiple functional roles? Evidence from single-unit recording of neurons in premotor areas suggests that there is a wide variety of neurons that respond to different contexts. For example, during the discovery of mirror neurons, many types of such neurons were identified (Di Pellegrino et al., 1992). Some of these are called "strictly congruent" mirror neurons, which respond to action observation and action execution only to the same exact movement. More common were "broadly congruent" mirror neurons, which respond to action observation and action execution during similar types of movements, encompassing a broader response range. We postulate that the first type is responsible for driving motor resonance-related activation, while the latter type could potentially underlie the sort of sensory prediction we discuss. Finally, a third type of neuron they observed was called a "canonical neuron", which respond to the observation of manipulable objects. Perhaps these neurons could play a role in mental simulation, or affordance processing. These examples are all speculative and not grounded by any evidence in the present work, but they aim to push intuitions toward a fresh perspective. Future work using single-neuron recording would be needed to directly test such hypotheses. At a brain region level, however, we can learn more by observing how activation in local regions changes with repetition of sensory stimuli or changes in stimuli.

Future research that we are currently engaged aims to explore how sensorimotor contingencies are learned by training participants on novel sensory to motor mappings. We will then use these controlled artificial mappings to explore sequential prediction and/or simulation using the motor system.

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