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Seeing, Acting, Understanding: Motor Resonance in Language Comprehension

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Observing actions and understanding sentences about actions activates corresponding motor processes in the observer–comprehender. In 5 experiments, the authors addressed 2 novel questions regarding language-based motor resonance. The 1st question asks whether visual motion that is associated with an action produces motor resonance in sentence comprehension. The 2nd question asks whether motor resonance is modulated during sentence comprehension. The authors' experiments provide an affirmative response to both questions. A rotating visual stimulus affects both actual manual rotation and the comprehension of manual rotation sentences. Motor resonance is modulated by the linguistic input and is a rather immediate and localized phenomenon. The results are discussed in the context of theories of action observation and mental simulation.

Keywords: language comprehension, action observation, mirror system, mental simulation, embodied cognition

What kind of perturbation in people's minds and brains does hearing or reading a sentence like "Eric turned down the volume" bring about? Classical cognitive science assumes that this will lead to the activation of abstract representations in long-term memory that will be integrated into a network representing the meaning of the sentence. The physical action of manual rotation is not part of such an abstract representation. A completely different answer to the question is inspired by current research on action observation and understanding. In contrast to the classical cognitive view, this new view predicts that the example sentence will activate a motor program for (counterclockwise) manual rotation in the listener or reader.

The rationale for this prediction lies in the phenomenon of *motor resonance*. When people observe someone else perform an action, the neural substrates are recruited that are active when they are performing that action themselves. Motor resonance has been observed in a wide range of studies and has been the focus of ideomotor theories (Greenwald, 1970; James, 1890; Jeannerod, 1994; Prinz, 1997). Many studies of motor resonance have been inspired by the recent discovery of so-called *mirror neurons* in the ventral premotor cortex of the macaque monkey (e.g., Gallese, Fadiga, Foggassi, & Rizzolatti, 1996). Single-cell recordings of neurons in the macaque monkey ventral premotor cortex fire when the monkey observes an action being performed that it also has in its own action repertoire (e.g., grasping a food item). These neurons have been termed *mirror neurons*. Mirror neurons have also been shown to fire when the monkey hears a sound associated with an action in its repertoire, for instance, cracking a nut (Kohler et al., 2002).

It is important to note that mirror neurons have been shown to be responsive to an understanding of the goal of an action. When the monkey knew there was food behind a screen, its mirror neurons responded when the experimenter's hand moved toward the food, even though it disappeared behind a screen. The activation pattern was similar to a condition without the screen; some mirror neurons responded equally strongly in both conditions, whereas others responded more strongly in the full vision condition. In contrast, this pattern of activation was not shown, with or without screen, if there was no food, but the experimenter made the same grasping movement (Umiltà et al., 2001). Thus, having a mental representation of the goal of a grasping action seems both necessary and sufficient for mirror neuron activation.

A recent computational approach (Keysers & Perrett, 2004) suggests how sensory information becomes associated with motor programs due to the anatomical connections between the superior temporal sulcus (STS) area, which responds to visual and auditory stimulation, and Areas PF and F5, which receive input from STS. Because a subset of neurons in STS shows some degree of viewpoint independence, the monkey learns to associate not only the sights and sounds of its own actions with motor programs but also the sights and sounds of the same actions performed by others. Converging evidence has been provided in brain imaging studies of humans (corresponding human areas: BA 44 and 6, posterior parietal lobe and STS). When humans observe a facial action that is within their repertoire (e.g., human or monkey lip smacking), an increased blood flow in the premotor cortex will occur. However, when a facial action is observed that is outside the human repertoire (e.g., barking), only activation of the visual cortex, but no activation of the premotor cortex, occurs (Buccino et al., 2004).

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The human mirror system appears to be more flexible than the monkey's in that it responds to a broader range of actions, including mimed ones in which no goal object is present, as well as to the visual presentation of manipulable objects (Grèzes, Armony, Rowe, & Passingham, 2003).

In addition to the single-cell recordings in monkeys and the human brain-imaging data, there also is behavioral evidence for motor resonance during action observation. In visually guided actions, task-specific anticipatory eye movements are required for planning and control. For example, when people are stacking blocks, they tend to fixate the pick-up location before they pick up the block and the landing location before they put down the block. Such anticipatory eye movements have also been found in subjects observing someone else stacking blocks (Flanagan & Johansson, 2003). This is evidence for motor resonance, because it suggests that the same visual-to-motor pathway that is active when people perform actions is active when people observe actions performed by others.

Findings such as these regarding motor resonance have given rise to theories of action understanding (e.g., Blakemore & Frith, 2005; Jackson & Decety, 2004; Jeannerod, 2001; Prinz, 1997; Rizzolatti & Arbib, 1998; Rizzolatti & Craighero, 2004; Wilson & Knoblich, 2005; Wolpert, Doya, & Kawato, 2003). One commonality among these theories is that they propose that action understanding involves the mental simulation of the observed action using the neural substrates that are involved in performing the action. It is assumed that the skill to mentally simulate others' actions derives from the ability to observe, predict, and control one's own actions. Being able to simulate the perceptual effects of one's own action provides a useful shortcut given the delay involved in sensory transmission (Decety & Chaminade, 2003; Wilson & Knoblich, 2005; Wolpert et al., 2003). An organism's interactions with the world lead to the development of sensorimotor contingencies. Once these contingencies are in place, an activated perceptual representation of a goal state can serve to guide the actions that bring about the desired perceptual effect (Hommel, Musseler, Aschersleben, & Prinz, 2001).

Language Comprehension

Theories of action observation have been extended not only to the domain of action understanding but also to the domain of language understanding (e.g., Gallese & Lakoff, 2005; Glenberg & Kaschak, 2002; MacWhinney, 2005; Rizzolatti & Arbib, 1998). The idea is that people understand linguistic descriptions of actions by mentally simulating these actions, just like people understand directly observed actions by others through mental simulation. On this view, language understanding can be conceptualized as the language-induced mental simulation of the described actions (see also Barsalou, 1999).

A first step toward developing such simulation-based theories of language comprehension is to examine whether language comprehension produces motor resonance. There are at least two levels at which this question can be posed. The first level is that of the form of the linguistic utterance. It has been demonstrated that hearing phonemes activates, in the listener's speech motor system, the same tongue muscles that are used to produce these phonemes (Fadiga, Craighero, Buccino, & Rizzolatti, 2002), a finding that is consistent with the motor theory of speech perception (Liberman & Mattingly, 1985).

More directly relevant to the focus of this article is the second level at which motor resonance might occur, namely that of the linguistic utterance's meaning. There already exists behavioral evidence that language comprehension produces motor resonance. For example, subjects who judged whether objects shown in pictures were natural or man-made by manipulating an input device that required either a power grip or a precision grip exhibited a response compatibility effect. Power grip responses were faster to pictures and words denoting objects that require a power grip compared with pictures and words denoting objects requiring a precision grip, whereas the reverse was true for precision grip responses (Tucker & Ellis, 2004, Experiment 3). The compatibility effect for words was comparable with that of pictures. Furthermore, hand shape may prime the comprehension of sentences describing the manipulation of objects (Klatzky, Pellegrino, McCloskey, & Doherty, 1989). These findings suggest that words make available the affordances (Gibson, 1986) of their referent objects.

There is also evidence that the comprehension of action sentences may involve motor resonance. Subjects who listened to sentences such as "He opened the drawer" and made sensibility judgments (Does the sentence make sense?) by pressing a button, which required either movement toward or movement away from their body, displayed an action-compatibility effect (ACE), such that responses were faster when the physical response was in the same direction as the movement implied by the sentence (Glenberg & Kaschak, 2002). For instance, responses made toward the body were faster after "He opened the drawer" than after "He closed the drawer," and the reverse was true for responses away from the body.

Recent neuroimaging studies have produced converging evidence. Motor regions of the brain are active during the comprehension of action words (Hauk, Johnsrude, & Pulvermüller, 2004) and sentences (Tettamanti et al., 2005). More specifically, both studies found that the areas of activation in the premotor cortex were somatotopically organized, such that sentences about mouth actions, hand actions, and leg actions each activated different areas, which in other studies have been associated with movement in these effectors. An important question is whether motor resonance is instrumental or ornamental to comprehension. That is, does motor activation affect comprehension, or does it occur simply as a byproduct of comprehension? A recent study using transcranial magnetic stimulation provides support for the former interpretation. When arm or leg areas in the left hemisphere received transcranial magnetic stimulation, lexical decisions to words denoting arm or leg actions were facilitated (Pulvermüller, Hauk, Nikolin, & Ilmoniemi, 2005).

Here, we investigated motor resonance in language comprehension in the context of manual and visual rotation. There is behavioral and neuroimaging evidence that visual mental rotation and manual rotation rely on overlapping neural substrates (e.g., Parsons, Fox, & Downs, 1995; Wexler, Kosslyn, & Berthoz, 1998; Windischberger, Lamm, Bauer, & Moser, 2003; Wohlschläger & Wohlschläger, 1998). Wexler and colleagues (1998) proposed that mental rotation should be viewed as covert manual rotation. They suggested that motor processes are not merely output processes but are a central part of cognition. As mentioned earlier, covert motor processes allow people to see the end result of a planned action (e.g., Wolpert et al., 2003). If manual and mental rotation rely on overlapping neural substrates, performing a manual rotation task should interact in very specific ways with a simultaneous mental rotation task. To test this hypothesis, Wexler et al. had subjects rotate a joystick at certain angular speeds while performing the Cooper-Shepard mental rotation task. They found that compatible rotation directions yielded shorter response times and fewer errors in the mental rotation task. In addition, the angle at which subjects rotated the joystick was correlated with the angle of mental rotation but only when the two rotation directions were the same. Furthermore, the speed of manual rotation was found to affect the speed of mental rotation. Brain-imaging research has provided converging evidence. The premotor cortex has been found to be active during mental rotation (Parsons et al., 1995; Kosslyn, Digirolamo, & Thompson, 1998; Windischberger et al., 2003).

This relation between manual and mental rotation allowed us to investigate two new questions of motor resonance in language comprehension. The first question concerns whether motor resonance during language comprehension can be elicited by a concurrent visual stimulus. This question is prompted by the notion of ideomotor theories that the visual effects associated with actions produce activation in the motor system that commonly produces the effect.

The second question we sought to address concerns the waxing and waning of motor resonance during online sentence comprehension. Thus far, behavioral studies on motor resonance in language comprehension have either used single words (Klatzky et al., 1989; Tucker & Ellis, 2004) or have assessed motor resonance at the end of a sentence as reflected in a judgment about the sentence rather than as an integral aspect of comprehension (Buccino et al., 2004; Glenberg & Kaschak, 2002). It is important to have more direct measures of motor resonance during online comprehension to gain a better understanding of its temporal contour: When does it start and when does it end?

We conducted five experiments to address these two questions. Experiments 1 and 2 lay the foundation for Experiments 3 and 5, which address the first research question. Experiments 4 and 5 address the second research question.

Experiment 1

The finding that manual rotation affects visual mental rotation suggests a relation between actual visual rotation and manual rotation. Theories of action understanding would explain this finding by assuming that sensorimotor contingencies between manual and visual rotation have developed through interaction with the environment. As a result, the percept of visual rotation should covertly activate the motor programs that bring about this visual effect. Experiment 1 was designed to examine this question directly in an effort to lay the foundation for our subsequent experiments. Subjects observed a rotating black cross on the computer screen and twisted a knob as soon as the cross changed color.

Method

Subjects. Thirty-two introductory psychology students from Florida State University participated in the experiment to satisfy a course requirement. Two subjects were eliminated from the analysis for having accuracy that was lower than the other subjects (accuracy $< 75\%$), which left 30 subjects (18 female); the subjects' average age was 18.8 (range = 18–32) years.

Apparatus. A knob of about 1-in. in diameter was mounted on a 4-in. ×8-in. ×1-in. box, which plugged directly into a keyboard, and was placed in front of the subject where a keyboard would normally reside. The knob was located on the top of the box such that it afforded rotation in the horizontal plane. The knob turned approximately 60° in either direction, and when it reached either of these positions, it produced the equivalent of a keypress. A set of springs inside the knob caused it to self-center on release. The knob was so small that it required subjects to use only their fingertips to turn it.

Stimulus. The visual stimulus was a rotating cross consisting of two perpendicular lines of equal length (approximately 3 in.) and width (approximately 0.125 in.). Black, red, and green crosses were created in Adobe Photoshop 7.0 and then rotated by 10° 36 times. During the experiment, these images were sequentially presented to give an observer the perception of a smooth, rotating movement. The cross rotated at a constant speed of 10° every 100 ms and was colored black when a response was not required. A color change consisted of nine, sequentially presented red or green images. Critical color changes occurred once during each rotation and when the cross was 40°, 120°, or 200° from its starting position. After each color change, the cross reverted back to black while continuing to rotate.

Procedure and design. Subjects responded to color changes in the cross by turning the knob in either direction. Half of the subjects responded to a red color change with a turn to the right (a clockwise response) and to a green color change with a turn to the left (a counterclockwise response), whereas the opposite was true for the other half. After each trial, subjects released the knob to its starting position. Visual rotation direction was manipulated between trials. Each subject responded to 36 color changes. This yielded a 2 (visual rotation direction) × 2 (match: congruence of manual and visual rotation) × 2 (list: the mapping of a color change to a response direction) design, with the first two factors manipulated within subjects.

Results

Subjects were included only if they scored more than 75% correct on the task. Outliers among the correct items were removed in two steps. First, response times less than 100 ms and greater than 1,500 ms were removed. Next, response times ± 2 *SD*s from a subject's condition mean were removed. In total, 1.4% of the observations were removed. For the analyses below, an alpha level of .05 was assumed.

The response times were subjected to a 2 (manual rotation direction) × 2 (match) × 2 (list) mixed analysis of variance (ANOVA). There was a main effect of match, such that compared with congruent rotations ($M = 653$ ms, $SD = 95$), incongruent rotations ($M = 671$, $SD = 98$) were 18 ms slower, $F(1, 28) = 7.93$, $MSE = 1{,}767$, $\eta_p^2 = .221$. In addition, there was a main effect for visual rotation direction, $F(1, 28) = 9.17$, $MSE = 2{,}680$, $\eta_p^2 = .247$; color changes during clockwise rotations ($M = 674$ ms, $SD = 101$) were detected more slowly than color changes during counterclockwise rotations ($M = 649$ ms, $SD = 91$). We are not sure why this occurred. There was no interaction between match and visual rotation direction ($F < 1$), meaning that there was no effect of manual rotation direction. Mean accuracy was 87% ($SD = 10$)

Discussion

This result shows that visual rotation affects manual rotation. Responses were faster if the manual rotation was in the same direction as the visual rotation and slower if the two directions differed. This finding is consistent with the hypothesis that observing visual rotation produces motor resonance.

Experiment 2

The results of Experiment 1 suggest that visual rotation produces motor resonance. If the comprehension of sentences describing manual rotation (e.g., “He turned down the volume”) produces motor resonance, then it should affect concurrent motor processing; same-direction rotations should yield faster responses than different-direction rotations, a variant of the ACE (Glenberg & Kaschak, 2002; see also Tucker & Ellis, 2004, Experiment 3). This prediction was tested in Experiment 2. Subjects listened to recordings of sentences and then made sensibility judgments about them. On critical trials, the sentences described manual rotation. Subjects indicated whether the sentence made sense by turning the knob either to the right for a yes response and to the left for a no response (half the subjects) or the other way around (the other half of the subjects).

Method

Subjects. Fifty-eight students (39 female) enrolled in introductory psychology courses participated for course credit. The subjects’ mean age was 18.3 (range = 18–21) years.

Stimuli and design. Thirty sentence fragments involving actions that typically require hand rotation were created and pilot tested. Twenty-two subjects in a pilot study were asked to indicate which direction their right hand would turn while performing the actions stated in each fragment. Their choices were *always counterclockwise*, *usually counterclockwise*, *always clockwise*, *usually clockwise*, *or N/A* (reserved for items with which the subject was unfamiliar or for actions that depended heavily on other factors). Of the original 30 items, 18 items (9 for each direction) were retained for use in the experiment. An item was eliminated if it was consistently unfamiliar to subjects (e.g., “using a rotary phone”) or if subjects did not share a consistent rotation orientation for it (e.g., “focusing a microscope”). Appendix A shows the items used in Experiment 2. None of the pilot subjects participated in the actual experiment.

The sentences were spoken by a native speaker of American English and digitally recorded with the Audacity (Version 1.2.1; see http://audacity.sourceforge.net/) media program. They varied in length from approximately 1,600 ms to almost 3,000 ms.

Procedure. The same knob box as in Experiment 1 was used to record the response times. Subjects made sensibility judgments by turning the knob in either direction. Half of the subjects responded to a sensible sentence with a turn to the right (a clockwise response) and to a nonsensical sentence with a turn to the left (a counterclockwise response). The reverse was true for the other half of subjects. Each subject responded to 72 randomly presented sentences (18 experimental, 18 sensible fillers, and 36 nonsensical fillers). After each response, subjects released the knob to its starting position.

There were three factors in the design of this experiment. Implied rotation direction (clockwise vs. counterclockwise) as expressed in the sentences was counterbalanced across subjects. Manual rotation direction (clockwise vs. counterclockwise) was manipulated between subjects.

Results

We removed two items based on a postexperiment questionnaire (“James set the washing machine” and “Troy twisted open the beer bottle”). The first sentence for some reason was judged nonsensical by almost half the subjects, and the second sentence did not receive a high counterclockwise rating, presumably because people may rotate the cap and the bottle at the same time in opposite directions. All subjects achieved at least 75% accuracy in the sensibility judgments ($M = 87\%$).

Response times were recorded from the onset of each auditorily presented sentence. To assess the judgment times, we subtracted the duration of each sound file from the response times (in some cases where a sensibility judgment was made before the end of the sound file, this led to negative judgment times). Outliers were removed as follows. First, response times shorter than −250 ms (i.e., 250 ms before the end of the sound file[1]) and times over 1,500 ms were removed. Subsequently, response times 2 *SD*s above or below a subject’s condition mean were removed. This resulted in the removal of 4.4% of the correct response times.

Subjects responded more quickly when the rotation implied by the sentence matched their response rotation ($M = 237$ ms, $SD = 108$) than when the two directions mismatched ($M = 275$ ms, $SD = 133$). This 38-ms difference was significant, $F(1, 57) = 4.28$, $MSE = 9{,}794$, $\eta_p^2 = .070$.[2] Clockwise manual responses ($M = 230$ ms, $SD = 104$) were faster overall than counterclockwise responses ($M = 281$ ms, $SD = 114$), a significant difference, $F(1, 56) = 4.01$, $\eta_p^2 = .067$. Apparently, a clockwise rotation can be made more quickly with the right hand than a counterclockwise rotation. There was no interaction between match and direction ($F < 1$). To explore the effect of rotation direction more directly, we examined responses to the correct filler items, that is, sensible sentences that did not imply manual rotation (e.g., “Tom signed the check”). Compared with clockwise responses ($M = 248$ ms, $SD = 139$), manual counterclockwise responses ($M = 308$ ms, $SD = 133$) were significantly slower, $F(1, 56) = 5.01$, $MSE = 11{,}937$).[3] This effect may be due to clockwise responses being more consistent with an affirmative “makes sense” judgment than counterclockwise responses.

Discussion

Sensibility judgments for manual rotation sentences were made more quickly when the manual response to the sentence was in the same rotation direction as the manual action described by the sentence. This extends the ACE (Glenberg & Kaschak, 2002; Tucker & Ellis, 2004) to the domain of manual rotation. It should

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[1] Subjects could respond before the end of the sound file. For example, if the last word ended with a nasal (e.g., /n/), its meaning would be known before the end of the sound file and so a response could be made.

[2] Item analyses were performed but were removed as requested by the editor. However, effects that were significant by subjects were also significant by items. The results of the relevant analyses can be obtained from Rolf A. Zwaan.

[3] One might be tempted to use the neutral item to assess facilitation or interference in the experimental items. However, we think such analyses are uninformative, because they are compromised by the fact that they would involve a comparison across different sentences.

be noted that the effect was smaller than the visual motor effect observed in Experiment 1. This is presumably due to the fact that the trials in Experiment 1 were rather uniform (color changes in a rotating cross), whereas there is inherently more variation in linguistic stimuli. We also found that clockwise manual responses were made more quickly than counterclockwise responses.

Experiment 3

Experiment 1 established that observing visual rotation produces motor resonance. Experiment 2 established that comprehending manual rotation sentences produces motor resonance, as evidenced by its effect on actual motor responses (the ACE). Experiment 3 examined the prediction that observing visual rotation affects the comprehension of manual rotation sentences.

Method

Subjects. Our criteria for subject inclusion were the following. We only included subjects who (a) responded 90% or more within the time limit to a color change[4] and (b) achieved a score of 75% or more correct on the sensibility ratings. Thirty-nine subjects (29 female) met these criteria, whereas 8 were removed from the analysis for failing to meet them. The subjects' mean age was 19.0 (range = 18–37) years.

Materials. The same sentences as in Experiment 2 were used (with the exclusion of "James set the washing machine" and "Troy twisted open the beer bottle"). The visual stimulus rotated at the same speed (10° every 100 ms for 3,600 ms) as in Experiment 1. Unlike in Experiment 1, there now only was one color change, from black to red.

Procedure and design. Subjects made sensibility judgments while concurrently monitoring the rotating cross for color changes. Subjects responded to a color change to red by pressing the spacebar and made sensibility judgments with the *F* and *J* keys. Subjects made 64 sensibility judgments (16 critical items, 16 sensible fillers, and 32 nonsensical fillers). A color change was always from black to red, occurred only during filler sentences, and occurred in 25% (i.e., 16 times) of the trials. There were three factors in the design. Implied rotation direction was counterbalanced across subjects. Visual rotation direction was varied within subjects. Finally, list was manipulated between subjects.

Results

As in Experiment 2, response times were recorded from the onset of each auditorily presented sentence. To assess the judgment times, we subtracted the duration of each sound file from the response times (in some cases where a sensibility judgment was made before the end of the sound file, this led to negative judgment times). First, response times shorter than −250 ms (i.e., 250 ms before the end of the sound file) and times over 1,500 ms were removed. Subsequently, response times 2 *SD*s above or below a subject's condition mean were removed. This resulted in the removal of 2.7% of the correct response times. Sensibility judgments were 53 ms faster when the rotation direction of the cross matched the rotation direction implied by the sentence ($M = 124$ ms, $SD = 138$) compared with when there was a mismatch ($M = 177$ ms, $SD = 177$), a significant difference, $F(1, 38) = 8.79$, $MSE = 12{,}461$, $\eta_p^2 = .188$. Counterclockwise sentences produced faster responses than clockwise sentences, $F(1, 38) = 10.87$, $MSE = 10{,}334$, $\eta_p^2 = .222$. However, given that the clockwise and counterclockwise sentences were not identical, this difference is not very meaningful. The two factors did not interact ($F\text{s} < 1$).

Discussion

We obtained a significant congruence effect of visual rotation on language-induced manual rotation. Comprehension of manual rotation sentences was easier when a concurrent visual stimulus was presented rotating in the same direction as the manual rotation implied by the sentences compared with a stimulus rotating in the opposite direction. This result shows for the first time, to our knowledge, that a visual stimulus interacts with the comprehension of sentences describing manual actions.

Experiment 4

Thus far, our experiments provided evidence that language processing may recruit motor processes in a global sense. That is, we have evidence for motor resonance in terms of sensibility judgments given at the end of the sentence. In Experiments 4 and 5, we sought to gain insight into the limitations of the effect. Specifically, we were interested in the modulation of motor resonance during online comprehension.

Two issues are important in this context. The first one involves the onset of the effect. Some theories argue that all contextual information, that is, information gleaned from the preceding linguistic input as well as information from the communicative context, becomes available immediately to the language processing system, rather than at syntactic boundaries (e.g., Chambers, Tanenhaus, Eberhard, Filip, & Carlson, 2001; Chambers, Tanenhaus, & Magnuson, 2004). Thus, these theories predict that motor resonance should occur as soon as the manual rotation direction is clear from the sentence context. On the other hand, motor resonance might not occur until the end of the sentence if it is part of a wrap-up effect, which is assumed to occur when all of the information from the sentence is integrated (Just & Carpenter, 1987).

The second issue concerns the duration of motor resonance. For example, assuming *turned down* in the sentence "Eric turned down the volume" triggers motor resonance, as would be predicted by the immediacy hypothesis, does this resonance extend throughout the reading of the noun phrase denoting the direct object? On the one hand, one could predict that it would extend, given that the action has not been described completely and given the fact that the ACE has been observed in sensibility judgments performed at the end of a sentence. On the other hand, one could predict that the effect will be restricted to the verb, given that the noun phrase shifts attention away from the action to the acted-on object (moreover, in the example, the volume is strictly speaking, not the acted-on object). Such a prediction could be derived from MacWhinney's (2005) perspective theory, which assumes that multiple perspective shifts occur across phrase boundaries within a sentence.

Experiments 4 and 5 were designed to examine these hypotheses. To this end, we developed a paradigm in which subjects read

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[4] This 90% accuracy criterion is more stringent than the 75% used in Experiment 1. The reason for this is that the color change detection task in Experiment 1 was more difficult, as subjects had to select one of two possible responses (clockwise vs. counterclockwise rotation of the knob), based on the nature of the color change (to green or red). In the present experiment, the subjects only had to press a key when a color change (always to red) occurred.

a sentence one frame at a time, with each frame showing between one and three words, by rotating a knob; each 5° of rotation made the current frame disappear and a new one appear. As in our previous experiments, the critical sentences described actions involving manual rotation. We constructed our materials such that there was always one target region in the sentence, at which a specific manual rotation direction was implied. An example of such a sentence is *To quench/his/thirst/the/marathon/runner/eagerly/opened/the/water bottle*, with slashes indicating the frame boundaries (see Appendix B). The target region in this sentence is *opened*. At this point, it is unambiguous that the action involves a counterclockwise rotation. Thirsty runners typically drink water from a bottle. Turning the cap in a counterclockwise direction typically opens water bottles. We divided our sentences into four regions. The first was the preverb region, which included the seven frames preceding the verb frame. Given that this region did not specifically imply a manual rotation direction, we expected there to be no effect of matching versus mismatching direction.

The second region was the target region, which was always the eighth frame. If sentence comprehension immediately produces motor resonance, then matching rotation directions should produce shorter reading times than mismatching directions. The third region was the frame immediately following the verb, and the fourth region was the last frame of the sentence. By examining these frames, we would be able to determine the extent of sympathetic activation during sentence comprehension. Is it a rather immediate and short-lived effect, or does it extend across word boundaries?

Method

Subjects. Sixty students (36 female) enrolled in introductory psychology courses participated for course credit. The subjects' mean age was 19.3 (range = 18–22) years. Three additional subjects who did not meet the 80% accuracy criterion on the comprehension questions were replaced.

Stimuli and design. The sentences from Experiments 2 and 3 were adapted such that the direction of rotation was as unambiguous as possible by the onset of the verb. All sentences were constructed so that they consisted of 10 frames. The 8th frame of each sentence contained the verb, the 9th contained an article, and the 10th contained the direct object. The sentences were designed so that the verb would be the target region with regard to the direction of manual rotation. Words were presented in black text on a white background, left justified in the center of the screen.

A knob with similar dimensions to that used in Experiments 1 and 2 was constructed to enable rotation-contingent, subject-paced text presentation. Like the knob in Experiments 1 and 2, this knob contained springs that returned it to the centered position when released. As the knob was turned from the center position, the computer logged a keypress response approximately every 5°. Manual rotation direction was manipulated within subjects. Implied rotation direction of the sentences was counterbalanced across subjects.

Procedure. Subjects read sentences by turning the knob in either direction. For the first half of the experiment, they turned the knob in one direction to proceed through the sentences, and for the second half, they turned the knob in the other direction. After each sentence, subjects released the knob to its center position. Each subject read 48 sentences (16 experimental, 32 filler) during the experiment. A yes–no comprehension question pertaining to the content of the immediately preceding sentence followed half of the filler items. Responses to these comprehension questions were made on a standard keyboard.

The experiment began with the subject seated in front of a computer monitor, a keyboard, and a knob box wired to the keyboard. After sitting, the subject laid the keyboard in his or her lap to answer comprehension questions. The knob remained sitting on the desk, centered in front of the computer monitor, for the duration of the experiment.

Before the experiment began, each subject completed 20 practice trials under the supervision of an experimenter. The experimenter made sure that subjects were turning the knob smoothly throughout the duration of a sentence instead of doing the task with repetitive, jerking motions. This was an important safeguard because the manual motion of subjects presumably needed to be as compatible with the content of the target sentences as possible. After the practice trials, every subject was judged to be able to do the task well enough to proceed.

A trial began with the knob at the center position and the first text block of a sentence presented on the screen. When the subject turned the knob in the correct direction for approximately 5°, the second text block was presented. When the subject turned the knob an additional 5°, the third text block was presented. This continued until the 10th text block, at which point the subject was either instructed to release the knob and wait for the next sentence or was presented with a comprehension question. A response to the comprehension question required a response on the keyboard.

Results

Reading times over 1,000 ms and reading times more than 2 *SD*s from a subject's cell mean were removed from the analysis; this involved 2.8% of the data. The average reading times per region are shown in Figure 1. They were subjected to a 4 (sentence region) × 2 (direction) × 2 (match) × 2 (list) ANOVA, with list being the only between-subjects factor. Of main interest to our hypothesis was a significant interaction between region and match, $F(3, 168) = 2.81$, $MSE = 3{,}272$, $\eta_p^2 = .048$. This interaction is due to the fact that there was a significant 22-ms match advantage in the verb region, $F(1, 56) = 11.04$, $\eta_p^2 = .165$, whereas there was no match effect in the preverb region ($F < 1$), the first postverb region ($F < 1$), or the sentence-final region ($F < 1$). Finally, not relevant to our predictions, there was a main effect of sentence region, $F(3, 168) = 8.06$, $MSE = 5{,}271$, $\eta_p^2 = .126$.

Discussion

These results extend those of Experiment 2 in two ways. First, they demonstrate, for the first time in the literature, an effect of sympathetic activation during the reading of sentences describing actions. Earlier studies (Buccino et al., 2004; Glenberg & Kaschak, 2002; Experiment 2 in the present article) examined motor resonance in responses to sentences presumably given after the sentence was read. The present data provide insight into the online modulation of sympathetic activation. They are consistent with the finding that affordances of referent objects have an immediate influence on sentence processing (Chambers et al., 2004). As we have shown here, this immediacy effect extends to the verbal description of actions not in the understander's immediate environment. Second, whereas earlier studies have used sensibility or action–nonaction judgments, the present experiment used comprehension questions and did not involve nonsensical sentences, thus creating a more naturalistic reading situation.

Experiment 5

Our final aim was to investigate whether concurrent visual rotation would produce a similar pattern of sympathetic activation to that of concurrent manual rotation, as shown in Experiment 4. Our software did not allow us to present a continuously rotating

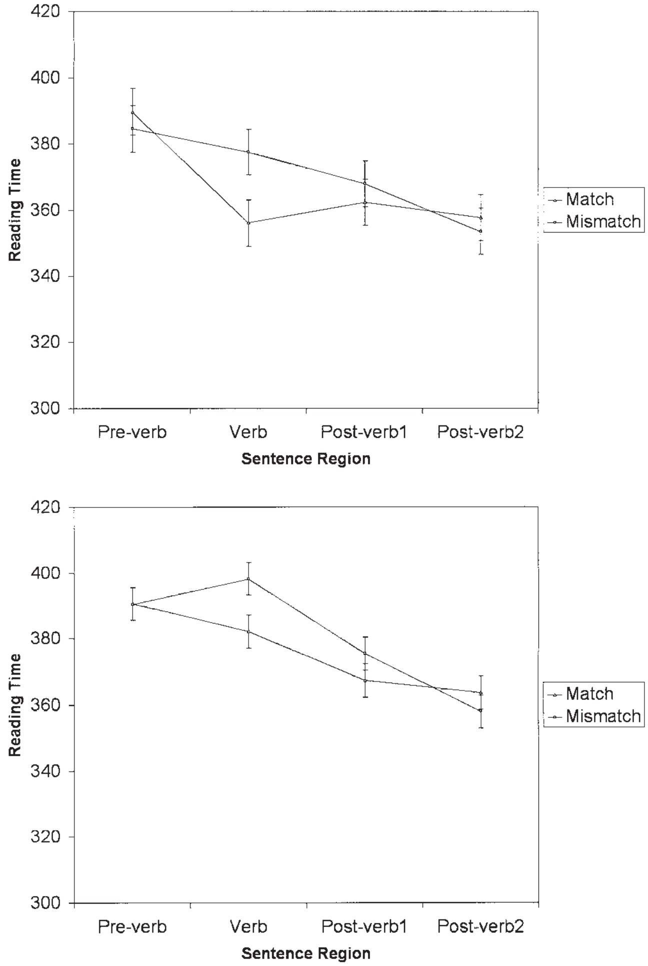

Figure 1. Average reading times per sentence region (with standard errors denoted by the error bars) for Experiments 4 (top panel) and 5 (bottom panel). Pre-verb = region preceding the target verb; Verb = target verb; Post-verb1 = the first word after the verb; Post-verb2 = the second word after the verb.

visual stimulus while at the same time presenting words and recording response times for several frames per sentence. We therefore decided to use an illusory rotation stimulus (see Figure 2), which created the percept of visual rotation but is stationary. It could therefore be presented as the background for the reading task, with the words being presented centrally on the screen.

Method

Subjects. Sixty students (42 female) enrolled in introductory psychology courses participated for course credit. The subjects' mean age was 18.8 (range = 18–20) years.

Stimuli and design. The same sentences that were used in Experiment 4 were visually presented in a subject-paced reading paradigm. The visual stimulus depicted 12 shaded half ovals that were situated in a circle such that they resulted in illusory visual rotation around a center point. Each word was left justified two characters to the left of that center point. This was judged by the experimenters to create the strongest visual illusion during normal reading. Figure 2 presents a sample image–text pairing used in this experiment.

The direction of rotation implied by the visual stimulus was manipulated within subjects and between items. Implied rotation direction of the sentences was manipulated within subjects and between items. List (groups of items appearing under the same condition) was manipulated between subjects and between items.

Procedure. The experiment began with the subject seated in front of a computer monitor and a keyboard. At the beginning of each trial, subjects were instructed to press the spacebar to continue. After the first spacebar press, the first block of text was presented. Each subsequent spacebar press resulted in the presentation of the next block of text until the sentence was finished. On one third of the trials, the subject answered a yes–no question regarding the content of the immediately preceding sentence. After each trial, subjects pressed the spacebar again to begin the next sentence.

Subjects read sentences by pressing the spacebar between blocks of text during the concurrent presentation of a visual stimulus. For the first half of the experiment, the visual stimulus depicted illusory rotation in one direction, whereas in the second half, it depicted illusory rotation in the opposite direction. Order was counterbalanced across subjects. Each subject read 48 sentences (16 experimental, 32 filler) during the experiment. Implied rotation direction was counterbalanced across subjects. A yes–no comprehension question pertaining to the content of the immediately preceding sentence followed half of the filler items. Each subject completed nine practice items before the experiment began.

Results

Five subjects were removed and replaced for having comprehension accuracy below 80%. We removed reading time outliers in two stages. First, latencies shorter than 100 ms and longer than 1,500 ms were eliminated. Next, latencies more than 2 *SD*s from a subject's condition mean were eliminated. In all, 2.6% of the data were eliminated. The remaining latencies were submitted to a 4 (sentence region) × 2 (match) × 2 (direction) ANOVA. The average reading times per region are displayed in Figure 1. Most relevant to our prediction, there was a significant interaction between sentence region and match, $F(3, 168) = 2.69$, $MSE = 2{,}031$, $\eta_p^2 = .046$. The matching sentences were read significantly faster in the verb region than the mismatching sentence, $F(1, 56) = 7.65$, $\eta_p^2 = .120$, whereas there was no match effect in any of the other three regions (Fs < 1.06). Not relevant to our predictions, there

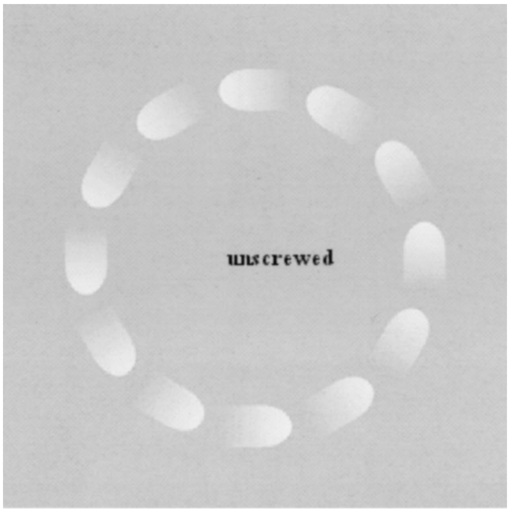

Figure 2. Illusory rotation stimulus used in Experiment 5.

also was a main effect of sentence region, $F(3, 168) = 12.95$, $MSE = 4{,}035$, $\eta_p^2 = .188$.

Discussion

The findings mirror those of Experiment 4 in important ways. Motor resonance during sentence processing occurred rather immediately and locally. That is, it was restricted to the target region. It is interesting to note that the reading times were considerably longer than those in Experiment 4. The difference may be due in part to the presence of the illusory rotation in Experiment 5. On the other hand, the reading times found in this experiment are comparable with keypress-based reading times that have been reported in the literature, suggesting that the illusion was not the main factor causing the difference in reading times between the two experiments. We believe that the main explanation lies in the fact that manual rotation is more fluent than keypressing. In fact, our own impression in pilot testing the manual rotation procedure was that it was surprisingly natural, an impression that was echoed by many subjects who participated in Experiment 4.

These findings extend those of the earlier experiments. They extend those of Experiment 3 by showing that the visual percept of manual rotation affects sentence processing online, rather than only during a sensibility judgment task, and they extend those of Experiment 4 in that the immediate and localized pattern of motor resonance was replicated using a visual paradigm.

General Discussion

The present study was motivated by two goals. The first goal was to examine whether concurrent visual information would produce motor resonance during the comprehension of action sentences. The second goal was to examine the modulation of motor resonance during sentence comprehension. Experiment 1 provided support for this assumption. We found that concurrent visual rotation affected manual rotation such that congruent rotations were facilitated relative to incongruent rotations. Experiment 2 examined the hypothesis that understanding sentences about manual rotation activates the neural substrates of manual rotation. In accordance with this hypothesis, we found that manual responses that were congruent with the action described in a sentence were faster than incongruent responses; this is an extension other ACEs reported in the literature (Glenberg & Kaschak, 2002; Tucker & Ellis, 2004). Experiment 3 showed that concurrent visual rotation affects the comprehension of sentences about manual rotation. Responses were faster when the two rotations were in the same direction than when they were in opposite directions. Together, these findings suggest that observing visual rotation and understanding sentences about manual rotation both engage neural substrates involved in actual manual rotation. Experiments 4 and 5 showed that the activation of these neural substrates during comprehension is an immediate and local affair. Motor resonance was observed only on the region of the sentence that unambiguously specified the rotation direction and did not extend beyond it.

There is an intriguing paradox between the findings of Experiments 2 and 3 on the one hand and Experiments 4 and 5 on the other. In Experiments 2 and 3 (as well as in those of Buccino et al., 2004, and Glenberg & Kaschak, 2002), motor resonance was found in decisions about the sentences that were presumably made after the sentences had been read. In contrast, the more fine-grained online measurements of Experiments 4 and 5 revealed that motor resonance had dissipated (or reversed direction, in the case of Experiment 5) before the end of the sentence. This paradox can be resolved if we assume that sensibility judgments involve a brief resimulation of the described action, thus producing renewed motor resonance. Such a two-stage explanation is consistent with the late assignment theory of syntax (Townsend & Bever, 2001), which assumes that sentence comprehension occurs in two stages. During the first stage, an initial meaning–form hypothesis is generated on the basis of lower level cues. During the second stage, a detailed syntactic structure is generated. Thus, one could hypothesize that Experiments 4 and 5 tapped the first stage, whereas the earlier experiments tapped the second phase. Because Experiments 4 and 5 were designed to be more naturalistic than the earlier experiments, they did not involve sensibility judgments (nor did they involve the presentation of nonsensical sentences); there only were comprehension questions on some of the filler sentences. The present experiments therefore do not provide a direct test of the two-stage hypothesis. This would involve using a sensibility judgment task combined with the reading-via-rotation procedure of Experiment 4. This combination would require the development of a new input device.

Experiments 4 and 5 showed that motor resonance was a rather immediate and short-lived effect with our stimulus materials. More detailed psycholinguistic work is needed to examine how generally applicable these conclusions are. This seems particularly true for the localized nature of the effect, given that the immediacy effect is consistent with other work on motor resonance (or rather, object affordances) in language comprehension (Chambers et al., 2004). We can advance two alternative hypotheses with regard to the localization of motor resonance. The first hypothesis is that the effect is intrinsically short lived. The second hypothesis is that the duration of the effect is modulated by linguistic context. In our experimental sentences, the target region in the sentence was the main verb, which was followed by a noun phrase describing an object. More often than not, this was not the object that was being rotated. For example, in opening a water bottle or gas tank, it is the cap that is being rotated. Thus, attention is being shifted away from the action to an object (which often was not rotating itself). There exist arguments that mental simulation is affected by multiple perspective shifts occurring within a sentence (MacWhinney, 2005). We are currently examining whether a more sustained focus on the rotating action leads to more sustained motor resonance.

At a general level, our results are consistent with recent theories of action understanding (e.g., Jackson & Decety, 2004; Jeannerod, 2001; Rizzolatti & Arbib, 1998; Rizzolatti & Craighero, 2004; Wolpert et al., 2003). These theories assume that people understand others' actions by mentally simulating them through the covert use of their own action repertoire. Visual information is relevant to mental simulations in that it engages motor programs that would bring about the observed visual effect (e.g., Hommel et al., 2001; Prinz, 1997).

Our findings have implications for theories of mental and manual rotation, for theories of mental simulation, and for theories of language processing. First, when taken together, these findings are consistent with the notion of a close link between manual and mental rotation. Previous research has provided evidence for the notion that visual mental rotation is covert manual rotation (Wexler et al., 1998). The present study shows that manual rotation systems are not only engaged during mental visual rotation but also during actual visual rotation. Moreover, the present study shows that visual rotation not only interferes with overt manual rotation but also with covert manual rotation. As Wexler and colleagues (1998) argued, showing a linear relation between mental and manual rotation is stronger than showing an interaction. Unfortunately, there are only so many rotation instances that can be described in sentences such that they (a) invoke similar mental simulations across subjects and (b) allow rotation to be described implicitly, so as not to focus attention on the nature of the experimental manipulation. This pair of constraints made it impossible for us to examine linear relations between language-induced covert manual rotation and overt manual rotation. On the other hand, it is extremely unlikely that subjects were aware of the rotation match or mismatch with some of the sentences. First, the rotation sentences were buried in a much larger set of sentences; only 25% of the sentences in Experiments 2 and 3 and 33% in Experiments 4 and 5 implied manual rotation.

Second, in Experiments 2 and 3, the ostensive task was to judge the sensibility of the sentences, and the nonsensical sentences were blatantly nonsensical, making the task a rather easy one. Likewise, the comprehension questions in Experiments 4 and 5 were easy to answer. In none of these experiments did the instructions make mention of manual rotation. Third, the manual rotation direction was never stated explicitly in the sentences. Fourth, and most important, when asked during exit interviews, none of the subjects in Experiments 2–5 reported noticing the relation between the content of some of the sentences and manual or visual rotation.

A limitation of the current study is that we focused on rather concrete action sentences. It could therefore be argued that although the current results point to a role of sensorimotor processes in sentence comprehension, they only apply to a very specific type of sentence and have no relevance beyond this. Although this criticism cannot be ruled out on the basis of the present data, it has been shown elsewhere how sensorimotor processes may be involved in more abstract forms of language comprehension. For example, a recent functional magnetic resonance imaging study showed that in human subjects secondary (but not primary) somatosensory cortex is activated both when the subjects themselves were touched and when they viewed movies of someone or something else being touched by objects (Keysers et al., 2004). In other words, somatosensory activation occurred even when two objects touched, suggesting that human observers understand objects touching other objects in terms of being touched themselves. It is interesting that this was not just an artifact of visual overlap, given that a movie of an airplane wing going over an island, although visually similar to a “touching” scene, did not yield the same pattern of somatosensory cortex activation. It has recently been proposed that the comprehension of abstract language is neurally realized by mental simulations, in which only a subset of the neurons are active that are engaged during the simulation of more concrete events (Gallese & Lakoff, 2005).

Although the experiments discussed in this article were behavioral, it is interesting to speculate on the neural substrates that may be involved in producing the effects shown here. One such area may be STS. As mentioned in the introduction, this area is involved in the cross-model integration information in action observation (Keysers & Perrett, 2004). This same area has been identified as part of a network, which also includes the superior temporal gyrus, responsible for the integration of spoken language and semantically congruent lip reading (Calvert, Campbell, & Brammer, 2000) and spoken and written language (van Atteveldt, Formisano, Goebel, & Blomert, 2004). For further theory development, it would be important to know if this network is also involved in the multisensory integration of auditory or visual linguistic input and semantically relevant nonlinguistic input.

The current results are consistent with those of several other studies, showing a strong connection between language processing and motor processes (e.g., Buccino et al., 2004; Chambers et al., 2004; Glenberg & Kaschak, 2002; Hauk et al., 2004; Klatzky et al., 1989; Pulvermüller et al., 2005; Tucker & Ellis, 2004). Together with a host of findings showing a strong connection between language and visual processes and representations (e.g., Bavelier, 1994; Fincher-Kiefer, 2001; Kaschak et al., 2005; Potter, Kroll, Yachzel, Carpenter, & Sherman, 1986; Richardson, Spivey, Barsalou, & MacRae, 2003; Spivey & Geng, 2001; Stanfield & Zwaan, 2001; Zwaan, Madden, Yaxley, & Aveyard, 2004; Zwaan, Stanfield, & Yaxley, 2002; Zwaan & Yaxley, 2003a, 2003b, 2004), as well as with studies showing a close connection between language and other somatosensory processes (Isenberg et al., 1999; Pecher, Zeelenberg, & Barsalou, 2003), these studies provide support for a simulationist view of language comprehension. On this view, comprehension does not involve the activation of abstract and amodal mental representations but rather the activation of traces of perceptual and motor experience. The present study provides some clues as to how these traces interact in the process of language comprehension.

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Appendix A

Sentences Used in Experiment 2

Counterclockwise

Dave removed the screw from the wall.
Mark turned left at the intersection.
Julia set the clock back.
Vincent dimmed the lights.
Troy twisted open the beer bottle.
Liza opened the pickle jar.
Bob opened the gas tank.
Eric turned down the volume.
John disconnected the cable from the TV.

Clockwise

Jim tightened the lug nuts.
Jane started the car.
The carpenter screwed the boards together.
Dennis turned on the lamp.
James set the washing machine.
Lucy took the highway’s exit ramp.
Jenny screwed in the light bulb.
Erin used the can opener.
Louis sharpened the pencil.

Appendix B

Sentences Used in Experiments 4 and 5

Clockwise

After driving/on the/highway/for/two-hundred/miles/he/exited/the/highway.

After/disposing/of the/burnt-out/light/the/projectionist/screwed in/the/new one.

To save/water/after/watering/the/garden/he/turned off/the/faucet.

His pencil/was dull/so/before/the/SAT/he/sharpened/his/pencil.

While/replacing/the tire/he/picked up/the wrench/and/tightened/the/lug nuts.

Before/the/big race/the driver/took out/his key/and/started/the/car.

To attach/the boards/he/took out/his/screwdriver/and/screwed in/the/screw.

The lamp/was off/and he/wanted/to read/so/he/turned on/the/lamp.

Counterclockwise

Craving/a juicy/pickle/he took/the jar/off the/shelf and/opened/the/jar.

While/at the/gas station/he/selected/unleaded/and/opened/the/gas tank.

He/realized/that the/music/was/too loud/so he/turned down/the/volume.

Having/recently/switched/to/satellite/TV/he/unscrewed/the/cable.

To quench/his/thirst/the/marathon/runner/eagerly/opened/the/water bottle.

While driving/to work/he/approached/the/intersection/and/turned left/onto the/street.

When/the annual/time change/in the/fall/occurred/he/set back/the/clock.

After/lighting/the candles/for the/romantic/evening/he/dimmed/the/lights.

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