

**When writing impairs reading:
Letter Perception's Susceptibility to Motor Interference**

Karin H. James^{1*} & Isabel Gauthier²

¹Indiana University, Bloomington, Indiana, 47405

²Vanderbilt University, Nashville, Tennessee, 37240

***Corresponding Author: Karin H. James**
Department of Psychological and Brain Sciences
Indiana University
1101 E. 10th St.
Bloomington, Indiana, 47405

khjames@indiana.edu

Abstract

We investigated how writing affects the concurrent visual perception of letters, using an interference paradigm. Participants drew shapes and letters while simultaneously visually identifying letters and shapes imbedded in noise. Experiments 1-3 demonstrated that letter perception, but not the perception of shapes, was affected by motor interference. This suggests a strong link between the perception of letters and the neural substrates engaged during writing. Both the overlap in category (letter vs. shape) and in the perceptual similarity of the features (straight vs. curvy) of the seen and drawn items determined the amount of interference. Experiment 4 demonstrated that intentional production of letters is not necessary for the interference to occur, because passive movement of the hand in the shape of letters also interfered with letter perception. When passive movements were used, however, only the category of the drawn items, (letters vs. shapes) but not the perceptual similarity, had an influence, suggesting that motor representations for letters may selectively influence visual perception of letters through proprioceptive feedback, with an additional influence of perceptual similarity that depends on motor programs.

The observable output of the brain is action: we convey internal processes through speech, locomotion, limb and eye movements and manipulation of the objects in our environment. These actions, in turn, allow sensory information to be gathered and processed to inform additional actions. In this sense, human behavior can be understood in terms of action-perception loops. Here, we consider how drawing and writing, and one's experience with writing, may influence the visual perception of letters.

The idea that our perception of the world is reliant on our motor interactions with our environment is not a new idea (e.g., James, 1890; Lotze, 1852), but one that has recently generated renewed interest, due in part to the theory of embodied cognition which emphasizes the role of interactions with the environment as a crucial aspect of cognitive processes (Barsalou, 1999; Clark, 1998; Johnson, 1987; Wilson, 2002). In this framework, actions influence perception not only externally, by modifying the perceived world, but also internally: executing a motor act, independent of its outcome, may affect perception through neural interactions (Wexler & van Boxtel, 2005). But how do the action and perception systems interact? Actions may be represented in terms of anticipatory codes of their (visual) consequences in the environment (James, 1890; Lotze, 1852). In addition, sensory events could engage action codes simply by virtue of the history of co-occurrences of the sensory and motor events (Hecht, Vogt, & Prinz, 2001; Prinz, 1997). Shared representations by the action and perception systems have been suggested in several theoretical frameworks for example, 'micro-affordances' shared by perception and action (Tucker & Ellis, 2001; Ellis & Tucker, 2001), the 'direct mapping' hypothesis of actions and perception (Gallistel, 1990), 'mental models'

incorporating action and perceptual processes (Schwartz, 1999) and the idea of forward internal models that can predict sensory consequences from efference copies of issued motor commands (Decety & Grezes, 1999; Miall et al., 2006). By virtue of the action and perception systems sharing representations in the brain, these hypotheses predict that under certain conditions, not only can perception affect action (a well known phenomena), but interestingly, motor learning and ongoing actions can affect visual perceptions.

The effects that actions have on perception can be divided into two types: effects observed when action and perception occur at the same time, and effects that past actions (experience) may have on subsequent perceptions. Actions that are performed at the same time as visual perception may result in interference of one system with the other, as each tries to access the same representation, or common codes. This could lead to a decrement in performance in visual perception, action, or both due to competition. In contrast, experience where action and perception are repeatedly paired may strengthen the common codes or representation and facilitate action and/or perceptual performance even when they are *not* performed concurrently. Evidence for both these situations has been demonstrated.

The influence of ongoing actions on visual perception has been studied using variations on interference paradigms. Musseler & Hommel (1997) showed that preparing to make a left-handed key press interfered more with responding to a left-pointing arrow than a right pointing arrow. Interestingly, this effect was only found when the interval between the action and the perception was very short. With considerably longer intervals, performance was facilitated when response hand and arrow direction

matched. The authors interpreted these results as demonstrating a temporary 'blindness' to stimuli that resembles the action, referred to as 'action-effect blindness' (Musseler & Hommel, 1997). Action-induced perceptual impairment was also demonstrated in a similar paradigm using drawing as the action and size perception as the visual task: when a small curve was drawn, a similar line was perceived as being larger, when a large line was drawn, the test stimulus was seen as smaller (Schubo, Aschersleben, & Prinz, 2001). Hamilton, Wolpert, and Frith (2004) also showed that performing an action altered perception in an interfering manner: holding a heavy weight biased people's judgements of a visually presented stimulus to be lighter. In a dual-task paradigm, Koch and Prinz (2005) demonstrated that visual encoding of a cue interfered with motor responses at very short intervals between stimulus and response but that as the interval was increased, the effect was diminished. Thus, the 'contrast effect' or interference (Schutz-Bosbach & Prinz, 2007), should only occur when the percept and the action are co-occurring. If the two events are separated in time, then the activation of one may facilitate the other.

Facilitation or 'priming' of action on perception and perception on action over a longer time frame has been documented. For instance, there is a large literature, going back at least as far as William James (James, 1890) suggesting a crucial role for action in perceptual learning. This includes studies as diverse as research on perceptual learning with stimulus deprivation (Held & Hein, 1963), adaptation to visual distortions by optical lenses (Held & Freedman, 1963; Held, 1965), infant learning about binocular depth cues (Gibson, E.J. 1969), the role of eye-movements in adult perceptual learning (O'Reagan & Noe, 2001) as well as computational studies of the advantages of "active

vision" -- how an observer (human or robot) is able to understand a visual environment more effectively and efficiently by acting on it (e.g., Lungarella, Pegors, Bullwinkle & Sporns, 2005; Lungarella & Sporns, 2005; 2006). In a similar vein, acting on novel objects during initial encounters can facilitate subsequent visual recognition of those objects (Harman, Humphrey, & Goodale, 1999; James, Humphrey, & Goodale, 2001; James et al., 2002). The perception of biological motion is also facilitated by prior performance of similar movements (Casile & Giese, 2006). In addition, participants can recognize an object faster if it is positioned in a manner congruent with how we typically act on the object (Tucker & Ellis, 2001). The degree or type of experience can determine to what extent action influence perception, for instance, the order of key presses can influence tone perception but only in skilled pianists (Repp & Knoblich, 2007).

Several neuroimaging studies have supported these behavioral findings: motor systems are automatically engaged upon visual perception of objects that have strong motor associations, such as tools, utensils, and letters (Chao & Martin, 2000; Gerlach, Law, Gade, & Paulson, 2002; Grezes & Decety, 2002; James & Gauthier, 2006; Longcamp, Anton, Roth, & Velay, 2003; 2005; Longcamp, Tanskanen, & Hari, 2006; Mecklinger, Gruenewald, Besson, & von Cramon, 2002). This activation does seem reliant on experience in some cases, as motor activation during the perception of notes was tied to expertise reading musical notation (Wong & Gauthier, submitted). Further, training individuals to practice writing novel, letter-like stimuli resulted in activation in letter sensitive regions, that was not apparent prior to extensive writing experience (James & Atwood, 2008). Children only develop a BOLD response to letters that is

specific to the fusiform gyrus after a specific type of experience involving motor system involvement (James, in press).

Whether action and perception interactions translate in interference or facilitation often seems to depend on temporal contingencies. Interestingly, there is also documentation of facilitation of perception during concurrent motor behavior. This curious effect has been shown mostly for mental rotation tasks. For instance, mentally rotating complex figures presented visually was facilitated by motor rotation of a joystick in the same direction as mental rotation, while movement in a incongruent direction slowed performance (Wexler, Kosslyn, & Berthoz, 1998). Mental rotation is also facilitated by manually rotating a block in the same direction and pulling a string from a spool (Schwartz & Holton, 2000). Presumably, the hand movement in these cases may help to solve the task, whereas in visual object recognition, hand movements may not play a role in the actual task of recognition. Facilitation has also been shown when perceiving body postures. In a dual-task paradigm, Reed and Farah (1995) demonstrated that perception of the body position of others was affected by one's own body position. More recently, Miall et al. (2006) showed that performed hand postures congruent with perceived hand postures facilitated performance in oddball detection tasks. Recognition of body parts and position may access a different neural system than object recognition. In fact, recent neuroimaging results suggest that body part perception does not overlap neurally with systems underlying object recognition (Downing, Jiang, Shuman, & Kanwisher, 2001). There is also strong evidence for mental rotation, orientation detection and perception of biological motion (Grossman et al., 2000) to be processed predominantly in the dorsal visual processing stream of the

cortex (Valyear et al. 2006; Gauthier et al., 2002; James & Gauthier, 2003). In contrast, visual object recognition is predominantly a ventral visual stream function. It is possible that interference effects are due to dorsal stream processing: during on-line control of action (Milner & Goodale, 1998) and during 'recognition' tasks that involve the dorsal stream.

Letters represent an interesting category with which to study questions of interactions between action and perception. Letters are read but rarely manipulated, although they are also written, and perhaps nowadays even more often, typed. Letter shapes do not 'afford' an action the way a brush or hammer does (Gibson, 1979) without any learning. That is, the form of the letter does not, by itself, suggest how we should interact with it. There is little work directly addressing whether objects without obvious affordances, but with motor associations, perhaps gained during learning, activate the motor systems during visual perception (when there is no concurrent action). Recently, we have shown that simply perceiving letters engages motor areas involved in writing letters (James & Gauthier, 2006; see also Longcamp et al., 2005). Similarly, learning to write novel letter-like forms results in activation of similar regions as letter perception, whereas learning these same forms without action results in activation common to other types of objects (James & Atwood, 2008). Behavioral evidence also supports the idea that motor experience with letters is stored and may be used during visual letter recognition. For instance, one's knowledge of the manner in which we write different strokes composing a letter affects its visual perception – our motor experience with these abstract forms can change our perceptions (Babcock & Freyd, 1988; Freyd, 1983; Kandel, Orliaguet, & Viviani, 2000; Knoblich, Seigerschmidt,

Flach, & Prinz, 2002; Orliaguet, Kandel, & Bois, 1997; Tse & Cavanagh, 2000). Training children to write letters also facilitates letter recognition, more so than training them to type letters (Cunningham & Stanovich, 1990; Longcamp et al., 2005). Pre-school children who practice printing letters show an increase in brain activity in the fusiform gyrus during letter perception, unlike children who practice saying letters instead of printing them, suggesting that motor training directly affects the visual representations of letters (James, in press). Such findings support the idea that information about actions with objects is stored with visual information, or at least, contributes to visual processing in some way.

In a similar way, recognition of movement is affected by past actions. Recognition of self-generated actions is very accurate, even long after the action has been produced, provided that velocity information is maintained in the re-enactment (Knoblich & Prinz, 2001). Movement can facilitate letter recognition in cases where performance is not yet, or no longer optimal. For instance, movement facilitates letter recognition in patients with pure alexia (a deficit in letter identification, Bartolomeo, Bachoud-Levi, Chokron, & Degos, 2002; Seki, Yajima, & Sugishita, 1995).

In the present study, we wished to address two issues regarding the effect of writing on letter perception. First, we ask whether concurrent motor behavior can affect visual processing of static forms, and if so, whether it is facilitatory or inhibitory. While it is interesting that perceiving letters recruits motor areas associated with writing (James & Gauthier, 2006; Longcamp et al., 2005, 2007), and that writing affects the ability to identify the movement produced during the formation of letters (Knoblich et al., 2002), it is unclear whether concurrent motor activity can interfere with the perception of static

letters (the way letters are usually encountered). Second, we ask if actions interfere with visual processing in a manner that reflects motor experience: in what ways do the content of the perception and the action have to match? In other words, how specific is the interaction, if it exists? Does the execution of any concurrent movement affect visual perception of letters, or is interaction limited to letters similar in shape, or even to the exact motor program associated with a letter? Writing is a highly practiced action in most adults and motor programs are precise enough for handwriting to have an individual signature, so there may be specific motor programs for writing different letters.

Experiment 1

In Experiment 1 we ask whether *any* movement affects visual perception of letters, or whether the movement has to be very similar to the perceived form. Of course, it is possible that just any concurrent movement will affect letter perception. But the interaction could also be more specific, in at least two possible ways. In one case, any motor act that is similar to a visually perceived form could affect perception – even if the motor act does not share the same cognitive category (letter or shape) as the visual stimulus. For instance, drawing a square or drawing the letter ‘F’ could equally interact with the visual perception of the letter ‘T’ simply on the basis of shared features. An alternative is that only a motor act that shares the same category as the visual form interacts. In this case, drawing a letter ‘C’ could interact more than a square with the perception of an ‘H’, not because of its similarity in production, but because it belongs to the same cognitive category – letters. The first possibility is more componential,

assuming a linked relationship between visual and motor units that represent the same part of a shape, while the second possibility is more categorical, assuming segregation of the motor programs for writing letters from those for other shapes. Of course, these two options are not exclusive, such that it would be possible for only motor programs of similar letters (but not other shapes) to interact with letter perception.

Methods:

Subjects

Thirty-five undergraduate students recruited from the Vanderbilt University undergraduate research pool were given partial course credit for their time. All participants provided informed consent and all reported normal or corrected to normal visual acuity. All subjects were right handed and included 16 males (mean age: 20.2 years) and 19 females (mean age: 20.9 years).

Stimuli

The visual stimuli were 6 uppercase letters imbedded in a 3" x 3" square of Gaussian noise presented on a grey background. The uppercase letters were constructed using the Sloan font (Pelli et al., 1988) and were an average of 2.5" x 2.5". Participants viewed the letters from a distance of approximately 30" and thus the stimuli subtended a visual angle of approximately 4.8 degrees. We included 3 'straight' letters: H, N and K; and 3 'curvy' letters: G, D, and U. Letters were presented for 500 ms with a 1000 ms inter-

stimulus-interval and were centered on the computer screen (see Figure 1 for examples of stimuli and design).

Apparatus

Stimuli were presented on an iMAC equipped with a CRT monitor, using RSVP software. Letters and shapes were drawn onto a Wacom Graphire digital writing pad, positioned to the right of the participant. The apparatus for visual presentation was the same in all experiments, and the apparatus for movement execution was the same for Experiments 1-3.

Procedure:

The general procedure for testing participants was the same in all experiments, and involved four stages. First, participants performed a letter identification task to determine their 75% contrast threshold for stimulus identification. This was done using a 2-up 1-down staircase procedure with letters presented in the Sloan typeface and imbedded in Gaussian noise with constant contrast. The 75% threshold was then estimated from a psychometric function fitted to the data. The mean contrast across participants was .055 (standard deviation = .0075), but each individual's contrast threshold for each stimulus was used to determine the stimuli to be used in the baseline letter identification task. The next stage was a baseline letter identification task. The purpose of this task was to measure letter identification abilities in each individual that would later be compared to their performance in the dual-task. The baseline letter identification task was administered using stimuli presented at four different contrasts:

one log unit and one/half log unit above the individual participant's threshold for each stimulus, and one log unit and two log units below this threshold. A range of contrasts was used to provide a range of difficulty across trials, and to prevent participants from becoming complacent. Contrasts were chosen such that accuracy was estimated to remain between 70-80%. Noise contrast was held constant across trials (RMS = .5). Signal (letter) contrast was varied across trials, with the values based on each participant's 75% identification contrast threshold. Letters at different contrasts were presented in random order – the presentation of the stimuli in the baseline task was the same as in the dual-task. During the baseline task, participants were asked to verbally identify visually presented letters imbedded in noise. Accuracy of letter identification was recorded by an experimenter sitting behind the participant and later compared against performance in the dual-task reported below. The experimenter who recorded the responses was blind to the specific predictions of the studies.

After performing the baseline identification task, participants were trained in the writing task-the third stage. Participants were asked to draw certain pairs of shapes or letters in alternation on a digital writing pad with a stylus, until writing was fluid and well practiced. This training, which took approximately 5 minutes, was performed for all letter and shape combinations used in the experimental session. In the final stage of testing, we began the experimental dual-tasks in which participants verbally identified letters in noise while writing specific letter or shape combinations. The visual identification part of the dual-task used the same procedure as the baseline letter identification task described above. In addition, participants had to simultaneously write or draw specified repeating sequences of letters or shapes. Participants were told that the letters and

shapes that they wrote and drew were recorded and would be part of the analysis, although this was not the case. This deception ensured that the participants were motivated to write/draw the correct letters and shapes. Participants only had to identify letters visually, but they concurrently drew either letters or shapes. This procedure resulted in 8 dual-task conditions, combinations of two visual conditions: see straight letters (H,N,K) and see curvy letters (D,G,U), and 4 drawing conditions: straight letters (W,Y), curvy letters (S,C), straight shapes (square, rectangle) and curvy shapes (circle, oval). The order of these conditions was counterbalanced across subjects.

Results and Discussion

We compared performance in each dual-task condition to performance in the baseline letter identification task, given these tasks only differed in terms of the writing/drawing component. For each participant and each stimulus, an interference index was computed using the difference in performance between the baseline and a dual-task condition. For instance, if performance was 85% in the baseline task, and 80% in the dual-task, the interference index would be 5. The interference index, therefore, reveals interference from the motor task, and more importantly allows a comparison of the degree of interference produced by different motor conditions. All analyses are based on this interference index - a higher number indicates higher interference from the concurrent motor task (raw % correct scores are recorded in Table 1).

A 2 (writing category [letters or shapes]) x 2 (writing curvature [straight or curvy]) x 2 (seeing curvature [straight or curvy]) repeated measures analysis-of-variance (ANOVA) revealed a main effect ($F(1,34)=11.7, p<.005$) of writing category, as drawing

letters ($M=7.3$) caused greater interference than drawing shapes ($M=3.0$). A significant interaction was also obtained between writing curvature and seeing curvature ($F(1, 34)=9.09$, $p<.005$). Drawing straight items interfered more with seeing straight letters than did drawing curvy items, and drawing curvy items interfered more with perceiving curvy letters than did drawing straight items (see Figure 2). There was also a trend toward a three-way interaction ($F(1,34)=2.7$, $p<.09$). This result, although not significant, suggests that the two-way interaction effect of congruency of the writing curvature and the seeing curvature (i.e., write straight and see straight or write curvy and see curvy) could be dependent on writing category, with stronger effects for writing letters than drawing shapes (see Figure 2). When single sample t-tests are performed comparing each interference value to 0 (no interference), all interference values when drawing letters are significant ($t(34)>2.7$, $p<.00625$, Bonferroni corrected), but only drawing straight shapes interfered significantly with perceiving straight letters, no other values when drawing shapes were significant ($t(34)<2.7$, ns).

The results of Experiment 1 suggest that motor activity interferes with letter perception. However, this result by itself is difficult to interpret because it may reflect a general dual-task cost (Kahnemann, 1973). More interesting is the modulation of this interference according to the nature of the visual and writing conditions. We found that writing letters interferes more with letter perception than does drawing shapes. This could reflect the categorical nature of motor programs for writing letters and their corresponding relationship to the visual representation of letters. Greater interference implies shared (Kahnemann, 1973) or interconnected (Kinsbourne & Hicks, 1978)

neural systems, supporting the notion that the visual representation of letters is not functionally independent from the motor representations engaged to write letters. However, because we did not have participants perceiving shapes, it is also possible that letters were somehow more taxing to write than shapes and would have interfered with any perceptual task. But we found that similarity in the shape of the visual and drawn stimuli mattered. For both writing letters and drawing shapes, stimuli that were congruent (in terms of curvature) with the shape of the visual letters caused more interference. Finally, there was a trend towards this latter effect occurring more when we write letters than when we draw shapes, but this could be due to a floor effect on the interference caused by shapes, which was lower overall than that caused by letters.

One interpretation of these findings is that the motor representations involved in writing letters interact with the visual representations engaged during letter perception. An alternate idea, however, is that participants may have sub-vocally rehearsed the items to draw, perhaps to keep track of where they were in the sequence of items to repeat. If so, interference may have occurred because of auditory rehearsal rather than from motor performance. Indeed, visual and auditory letter perception have been shown to interact in the brain (van Atteveldt, Formisano, Goebel & Blomert, 2004). Although it seems unlikely that covert verbal rehearsal would happen more for letters than shapes, in Experiment 2 we addressed this possibility. In addition, the trend towards a three-way interaction was re-examined using a more detailed analysis of the effect of curvature on interference.

Experiment 2

There were three motivations for Experiment 2. First, we reduced the number of letters or shapes to draw to one at a time. We hoped that drawing only one letter or shape would reduce the need for covert rehearsal. Second, we changed the viewed stimuli to completely curvy or completely straight. That is, curvy letters were composed of only curved line segments and straight letters were composed of only straight-line segments. Third, we changed the stimuli that were drawn so that we had a continuum of curvature similarity among the drawn and perceived letters. Unfortunately we do not have enough control over these properties of letters, given the limited set, to allow a perfect parametric manipulation.

Participants

Participants were drawn from the undergraduate research pool at Vanderbilt University and received partial course credit for their time. Only right-handed individuals that reported normal or corrected to normal visual acuity participated. Of these participants, 18 were male (mean age 20.2 years) and 17 were female (mean age 19.9 years), resulting in 35 total participants.

Stimuli

The visual stimuli were generated and presented as in Experiment 1, but included only the uppercase letters H, F, I, C, O, and U. Contrast thresholds were collected using the same procedure as Experiment 1. Mean contrast across subjects was similar to Experiment 1 ($M=.060$; $sd=.009$). The items to draw included the letters S, V and lowercase t and the number 8, as well as a circle, triangle, cross and infinity sign. We

used these stimuli for the following reasons: seeing the letter 'O' and drawing a circle resulted in the same shapes with different labels and belonging to different categories (letter and shape). In addition, the letter 't' and the Christian cross were also the same shape, but again belonged to different categories. These contrasts allowed us to better determine whether interference is due to feature or category similarity. We also now had a continuum of similarity: the letter t and the cross are more similar to the viewed letters H, F and I, (all composed of horizontal/vertical segments) whereas the written letter V and a triangle are not as similar (diagonals). These contrasts allow a comparison of similarity within the same category of "straight shapes".

Results and Discussion.

We again performed a 2 (writing category [letters or shapes]) x 2 (writing curvature [straight or curvy]) x 2 (seeing curvature [straight or curvy]) repeated measures ANOVA on the interference index. Results from this analysis revealed that writing letters ($M=9.6$) interfered more with letter perception than did drawing shapes ($M=6.8$) ($F(1,34)=10.52$, $p<.005$) (see Figure 3). However, a significant two-way interaction was again obtained ($F(1,34)=43.2$, $p<.001$): Congruent curvature between the perceived and the drawn stimulus led to more interference relative to incongruent curvature. The three-way interaction was also significant ($F(1,34)=4.8$, $p<.05$). For both writing letters and drawing shapes, feature congruency had a significant effect on interference. However, the effect was more pronounced during letter writing than shape drawing (see Figure 3). Single sample t-tests revealed that all drawing conditions in this experiment significantly interfered with letter perception ($t's(34)>2.7$, $p<.00625$, Bonferroni corrected).

Three planned comparisons were conducted, all of which involved selected items. The purpose of the first contrast was to determine if writing/drawing the same form produced different effects when the instructions placed that form in different writing categories. Specifically, we contrasted the conditions when subjects wrote a 't' vs. drawing a 'cross'. Results demonstrated that writing a 't' ($M=8.1$) interfered more with letter perception than did drawing a 'cross' ($M=3.1$) ($t(33)=3.11$, $p<.001$).

The purpose of the second contrast was to investigate whether or not there was a graded effect of similarity between the written and perceived stimuli. To do this, we compared the interference index across writing/drawing the four "straight" items while seeing the letters "F", "H" and "I". As depicted in Figure 4, all conditions interfered with straight letter perception more than chance (all conditions different from 0 baseline $p<.00625$, Bonferroni corrected). Furthermore, writing a 't' interfered the most with straight letter perception, followed by a cross, a v and a triangle, although the cross and v did not differ significantly from one another (all comparisons $p<.00625$, Bonferroni corrected). Therefore, perception of the straight letters was interfered with to different degrees depending on whether the drawn stimulus was a letter *and* depending on degree of curvature. These results suggest additive effects of feature and category similarity. The featural and categorical effects may depend on different resources, according to Sternberg's additive factors logic (2001), with all the associated caveats.

The third contrast of interest was comparing amount of interference on the perception of the letter 'O' when drawing a circle in comparison to other curvy shaped stimuli. Drawing a circle interfered much less ($M=1.0$) with perception than any of the other drawing conditions. In fact, this amount of interference was not significantly

greater than 0. Drawing the other curvy shape (infinity) led to more interference with 'O' perception (mean=12), as did writing curvy alphanumerics ('8' mean=11 and 'S' mean=11.3). The curvy shape and alphanumerics did not differ from one another ($t(33) < 1.2, ns$). Although this is based on a single case, it suggests that when the drawn item is exactly the same shape as the perceived item, little interference occurs. This was an unexpected result but past research suggests that a certain amount of motor priming can occur when drawn and perceived stimuli are the same (Craighero, Fadiga, Rizzolatti, & Umiltà, 1998). In this study, drawing a circle did not facilitate the recognition of 'O', but unlike the other stimuli, it did not interfere either. It is unclear whether this results from two opposite influences. This was not the focus of our study but could be an interesting avenue for future work.

The results of Experiment 2 support and extend those of Experiment 1. Again, interference depended on similarity of curvature and this time the effect was significantly larger for drawn alphanumeric characters. Both our omnibus ANOVA and planned comparisons suggest additive effects of overlap in item category (more interference of drawn alphanumeric characters than from shapes on letter perception) and of the similarity of the items. In addition, items that are exactly the same in shape may not interfere with perception, but items composed of the same features in a different combination do interfere.

Although this experiment was partially aimed at reducing the effects of covert verbal rehearsal, it does not rule out this possibility entirely. However, we assume to have eliminated the need to rehearse the items in order to support performance (to help participants keep track of which item to write next). In addition, because interference

primarily occurred for writing over drawing shapes, this verbal rehearsal would need to be more important for letters. It is possible that sub-vocalization of letter names specifically occurs automatically, a phenomenon not inconsistent with the general multimodal framework in which this work is inscribed. However, it is unlikely that verbal responses would mediate the effect of similarity in curvature that we observed.

We originally hypothesized that letter perception would be influenced by writing letters more than by drawing shapes because of our extensive experience writing letters. Experiments 1 and 2 confirm this hypothesis, but they do not address the possibility that writing letters could also interfere more than drawing shapes with perception of any other objects. To address this issue, we compared letter perception with shape perception in Experiment 3.

Experiment 3

In Experiment 3, we asked participants to perceive not only letters in noise but also shapes in noise. Participants' individual contrast thresholds were collected separately for letters in noise and shapes in noise and stimuli were generated based on these separate thresholds. We hypothesized that the effects seen in Experiments 1 and 2 with letter stimuli would not surface with shapes. We attributed our motor interference results to our extensive experience with writing letters. Although we do draw shapes, our motor experience is not nearly as extensive as with letters, thus shape perception should be less sensitive to motor interference than letter perception.

Participants.

Participants were drawn from the undergraduate research pool at Vanderbilt University and received partial course credit for their time. Only right-handed individuals with normal or corrected to normal visual acuity participated. Of these participants, 18 were male (mean age 19.9 years) and 17 were female (mean age 20.1 years), resulting in 35 total participants. All participants provided written informed consent.

Stimuli.

The letters that were viewed and the letters and shapes that were drawn in Experiment 2 were also used in Experiment 3. In addition, we included shapes imbedded in noise for visual identification: star, hexagon, square, heart, clover, and circle, resulting in 3 straight and 3 curvy shapes.

Procedure.

The procedure was the same as in the previous experiments with the exception that we acquired a second set of contrast thresholds for the shapes in noise, used as the extra baseline identification task for shapes in noise, and added 'shape perception' dual-task blocks. Collecting thresholds for shapes as well as letters allowed us to match visual identification difficulty for letter and shape identification by presenting shapes at a higher contrast than letters. Mean contrast across participants for letters was similar to Experiments 1 and 2 ($M=.058$; $sd=.0091$). Mean contrast across participants for shapes was higher than for letters ($M=.174$; $sd=.0194$). However, similar to letters, the contrast thresholds did not differ among the individual shapes. Participants first completed the

threshold task for letters and shapes, then completed the baseline letter and shape identification tasks, followed by the dual-task portion for letter and shape perception.

Results and Discussion.

We first performed a 2 (seeing category [letters or shapes]) x 2 (writing category [letters or shapes]) x 2 (writing curvature [straight or curvy]) x 2 (seeing curvature [straight or curvy]) factorial ANOVA on the interference index. There was a main effect of seeing category ($F(1,34)=108.9, p<.0001$): that is, interference on letter perception ($M=7.25$) was greater than interference on shape perception ($M=1.6$). There was also a main effect of stimulus drawn ($F(1,34)=14.4, p<.001$), as writing letters interfered more with perception ($M=5.8$) than drawing shapes ($M=2.7$) (see Figure 5).

The expected three-way interaction between perceived stimulus category and drawn stimulus category was significant ($F(1,34)=56.8, p<.0001$). To further investigate this effect, we ran separate 2-way ANOVAs on letter and shape perception. In letter perception, there was a significant main effect of writing letters vs. drawing shapes ($F(1,34)=13.9, p<.001$) as writing letters interfered more with letter perception ($M=10.4$) than did drawing shapes ($M=4.1$). In contrast, during shape perception, there was no main effect of the writing/drawing condition ($F(1,34)=.34, ns$). Writing letters interfered more with letter perception than did drawing shapes, while writing letters or shapes had no effect on shape perception.

We also obtained a four way interaction including all factors ($F(1,34)=38.15, p<.0001$). In general our 4-way interaction reflected the finding that during letter perception (see Figure 5a), congruency effects emerged as in the previous two

experiments. When viewing a straight letter, there was more interference from writing straight letters, but when viewing curvy letters there was more interference from writing curvy letters. This also held true for drawing curvy shapes during curvy letter perception, which interfered more than drawing straight shapes. Drawing straight shapes resulted in no interference with straight letter perception however ($t(34)=.77$, ns). The data from shape perception (5b), revealed only one interference score as significant: when writing letters, curvy shape perception is affected ($t(34)=3.05$, $p<.05$).

Additional planned contrasts were performed similar to Experiment 2. We again compared the amount of interference that resulted from drawing stimuli that differed from the seen stimuli (see Figure 6). Letters interfered more overall, but t's and v's did not differ from one another ($t(34)=3.2$, ns); and within drawing shapes, crosses interfered more than triangles ($t(34)=2.0$, $p<.05$). There was again greater interference from writing a 't' ($M=12.1$) on letter perception than drawing a cross ($M=3.5$) ($t(34)=2.4$, $p<.01$). Certainly in this experiment, writing straight letters interfered more with straight letter perception than did drawing shapes. Drawing shapes that were similar to the perceived letter (the cross) however, did interfere more with perception than did drawing dissimilar shapes (triangle).

As in Experiment 2, we found very little interference from drawing a circle on perception of the letter 'O' ($M=.45$, not significantly different from 0), but again more interference from drawing other curvy shapes ($M=6.4$), and the most interference from drawing curvy alphanumeric (8 $M=10.2$; 'S' $M=11.3$). Interestingly, there was a significant difference between drawing curvy shapes and drawing the letter 'S' ($t(34)=2.5$, $p<.01$), a reflection of the higher interference of writing letters than drawing

shapes on letter perception. When we look at interference effects on the perception of the circle, we see no significant interactions from either drawing shapes or from writing letters ($t(34) < 2.7$, ns).

Results from Experiment 3 confirm and extend our previous findings. The primary result of interest that emerges from Experiment 3 however, is that although we see significant interference of motor tasks on letter perception, motor interference is very low during shape perception. This allows us to reject the possibility that results in Experiments 1 and 2 were due to drawing letters simply being more difficult than drawing shapes. This supports the idea that motor interference that is observed on letter perception may depend on our extensive experience of writing letters. While letters are not the only visual stimuli with motor associations (tools, utensils and musical instruments are good examples), they are more strongly associated with practiced movements than are many common shapes, such as stars or hearts.

The category specific pattern of interference obtained here suggest that letter perception and letter writing engage overlapping (or at the least interacting) neural systems, consistent with prior fMRI work (James & Gauthier, 2006; see also Longcamp et al., 2005, 2006) and with frameworks that hypothesize shared representations (Prinz, 1997). In contrast, shape perception and shape drawing may be more independent from one another: the 'content' of these two types of stimuli may be sufficiently different as to not overlap (Prinz). But it should be noted that drawing shapes interfered more with letter perception than writing letters interfered with shape perception. Thus, what may be critical for this asymmetry is not so much the motor programs engaged during drawing, as they may be equally required when we draw shapes and write letters, but

the fact that motor areas may be engaged automatically by letter perception (James & Gauthier, 2006) but not by drawing shapes.

In the next study, we address to what extent the 'intent' or motor program that is recruited to write a letter interferes with perception, or whether information from the hand movement itself, such as proprioceptive information, is sufficient to interfere with letter perception. The fact that we obtain categorical effects (relatively dissimilar alphanumeric characters causing more interference than equally dissimilar shapes) suggests that at least part of the effects we observed may occur at a more abstract level. Nonetheless, across all three experiments we find robust effects of similarity of the features and it is possible that this reflects bottom-up mechanisms (muscle fatigue or proprioception) rather than top-down mechanisms (motor programming). Experiment 4 investigates this idea.

Experiment 4

To investigate whether results of Experiments 1-3 were due to top-down vs. bottom up mechanisms, we devised a task where the motor component of the experiment was either 'active' or 'passive'. This experiment also further addresses the issue of silent verbal rehearsal of letters. In the 'passive' condition, participants were unaware of the identity of the movements they were producing, and even if they recognized them, there was no need for them to rehearse the identity of the letters or shapes that were being written. Intentional motor acts differ from unintentional motor acts in many ways and although both result in proprioceptive feedback, there is

evidence that this feedback differs depending on intentionality (Paillard & Brouchon, 1968). For instance, in our passive condition, there should be no sense of authorship, in that the participants know that their hand is moving, but the movement is not intentional. According to some researchers, this unintentional movement will result in a different type of binding with the outcome of the action (Haggard, Aschersleben, Gehrke, & Prinz, 2002) and does not require prediction of action or awareness of outcome. There is evidence suggesting that the sensory consequences of our own actions are identified and attenuated (Blakemore, Wolpert & Frith, 2000), which would distinguish our active and passive conditions. Thus, forward model theories propose that the brain predicts the next sensory state based upon its current state and active motor commands (e.g., Wolpert et al., 1995). Because no writing motor command is issued in our passive condition, forward prediction should not be engaged. Thus, according to this model, passive movement should not interfere with perception in this task.

Separating intentional (active) and unintentional (passive) movements during our dual-task may help to determine at what level the visual-motor interferences occur. One interesting possibility we can address in this design is that different types of interference may have different causes. In previous experiments, we observed that interference obeyed a categorical boundary, writing a letter with a different identity than the letter on the screen could interfere with its perception, but not drawing a shape even when it was similar to the letter on the screen. Motor programs are likely to be categorical, while proprioception should be domain-general. Thus, in the passive condition, bottom-up proprioceptive information may be expected prior to a category assignment, and therefore might equally interfere on the perception of letters and shapes. In contrast,

categorical interference based on whether the item is a letter or shape may be more top-down and we would predict categorical interference only when letter writing is intentional, as in our prior experiments. Featural interference, on the other hand, may be independent of category assignment and we may therefore expect this type of interference under both conditions.

Participants.

Participants were again drawn from the undergraduate research pool at Vanderbilt University and received partial course credit for their time. Only right-handed individuals with normal or corrected to normal visual acuity participated. Of these participants, 12 were male (mean age 21.2 years) and 12 were female (mean age 20.9 years), resulting in 24 total participants. The participants provided written informed consents and were randomly assigned to one of two groups: active motor movement or passive motor movement.

Stimuli.

The perceived and drawn stimuli were the same as Experiment 3.

Apparatus.

To enable us to compare 'active' vs. 'passive' writing and drawing we constructed an apparatus that allowed an experimenter to move a participant's hand without requiring any knowledge or effort on the part of the participant (Figure 7). The experimenter 'wore' one part of the apparatus, while the other part was attached to the participant's

hand and wrist. A curtain separated the experimenter from the participant so that the participant could not see what the experimenter was doing. In the passive condition, the experimenter moved their portion of the apparatus and the participant's hand thus moved in the same manner. The experimenter either wrote letters or drew shapes depending on the experimental block. In the 'active' condition, the participants still 'wore' the yoked apparatus, but the experimenter did not, however, the apparatus was weighted such that the resistance on the participant's hand and arm in both conditions was similar.

Procedure.

After initial threshold determination and baseline letter and shape identification tasks (as in previous experiments mean contrast thresholds for letters ($M=.054$; $sd=.008$) and shapes ($M=.172$; $sd=.0192$) did not differ between Experiment 3 and 4), the experimenter explained how the yoking apparatus worked. The active and passive conditions were run as a between participant factor. Both sets of participants were trained in drawing and writing stimuli with the yoking apparatus. The stimuli used during training were different from those used for the actual experiment. Thus, the only difference between groups was that in the active group, participants were told what to write/draw and were required to do so during testing (similar to previous experiments). However, in the passive group, participants were told to try to disregard that their hand was being moved remotely by the experimenter and to simply concentrate on the letter and shape identification task. Participants reported that after an initial familiarization with the apparatus that they were able to disregard their hand movements successfully.

Verbal responses were recorded in both conditions by a second experimenter seated in the testing room.

Results and Discussion.

We performed a 2 (write condition [active or passive]) x 2 (seeing category [letters or shapes]) x 2 (writing category [letters or shapes]) x 2 (writing curvature [straight or curvy]) x 2 (seeing curvature [straight or curvy]) mixed model factorial ANOVA with the write condition (active or passive) run as a between-subjects factor, all other factors were within-subject.

Results from this ANOVA revealed significant main effects of category seen (letters vs. shapes) ($F(1,24)=58.2, p<.0001$) and category written ($F(1,24)=3.9, p.05$). There were no main effects of the curvature dimension, and interestingly, there was no significant main effect of the writing condition (active [$M=2.3$], passive [$M=1.9$]) on perception.

Interestingly, although not expected, writing condition (active or passive) and writing category (letters or shapes) interacted. While drawing letters interfered more with perception (active: $M=2.8$, passive: $M=2.8$) than drawing shapes (active: $M=1.8$, passive: $M=.99$) ($F(1, 24)=3.9, p<.05$), only drawing letters was sensitive to the writing condition, with more interference in the active condition. As expected, there was an interaction between seeing letters or shapes and drawing letters or shapes ($F(1,24)=23.3, p<.0001$). When letters were identified, there was more interference from writing letters ($M=5.7$) than from drawing shapes ($M=2.4$), but when shapes were perceived there was no interference from letter writing ($M=-0.13$) or from drawing

shapes ($M=.39$). This result replicates findings from Experiment 3. A 5-way interaction between all our factors ($F(1,24)=5.2$, $p<.03$) also surfaced, but because there was clearly no interference from writing when shapes were viewed (as evidenced in the 4 way interaction above), we ran an additional 4-factor ANOVA, (write condition, active vs. passive X write category, letters vs. shapes X write curvature (curvy vs. straight) X see curvature), excluding the shape perception condition. As depicted in Figure 8, the overall interference in this experiment was less than that in Experiments 2 and 3, but quite similar to Experiment 1. The variability in the amount of interference may stem from a combination of slightly lower baseline measures in this experiment than experiments 2 and 3 together with slightly better performance in the letter writing dual-tasks (see Table 1). Critically, the pattern of interference obtained in the active condition is the same as in all our other experiments.

The results of this ANOVA revealed only one main effect, that of the category of stimulus written, letters or shapes ($F(1,48)=20.4$, $p<.0001$). In addition, there was only one significant interaction, a 3-way interaction between written stimulus category, written stimulus curvature, seen stimulus curvature ($F(1,48)=4.4$, $p<.05$). A 2-way ANOVA revealed no effect of stimulus written on shape perception ($F(1,34)=.69$, ns) unlike the effect on letter perception ($F(1,34)=7.9$, $p<.05$). Figure 8 depicts this effect: There was much less interference on letter perception for both groups when shapes were drawn than when letters were written.

The active and passive conditions were similar in that they both produced significant interference from letter writing, but little, if any interference from shape drawing. This could happen if in the passive condition, participants recognized what

their hand was made to draw or write, or at least recognized it was more or less similar to writing letters. Interestingly, this effect does not have to occur very rapidly, because in our design it is impossible to tell if interference on perception comes from the simultaneously performed action, or those that occur prior in time. Depending on the temporal dynamics of the effect in the active condition, for instance if the proprioceptive feedback is categorized *and then* interferes, then the same effect could occur in the passive condition. Our experiment does not allow us to determine the temporal dynamics of the interference or to determine the specific locus of the interference common to both the passive and active condition. The fact that some interference can be obtained at all during the passive condition is interesting and argues against strategic factors being in cause. Nonetheless, the active vs. passive manipulation is most informative when it comes to the differences obtained in these conditions, to which we turn to next.

In the active condition, there was a robust congruency effect. Writing straight letters interfered more with perception of straight letters than writing curvy letters ($t(24)=3.2$, $p<.01$) and writing curvy letters interfered more with the perception of curvy letter than did writing straight letters ($t(24)=2.0$, $p<.05$) (Fig 8a). But when participants were identifying shapes, there was little interference from the concurrent motor task. In the passive condition (Figure 8b), however, the congruency effect was absent. Writing straight or curvy letters did not differ in their interference effect on straight letter perception ($t(24)=.5$, ns.) nor did they differentially effect curvy letter perception ($t(24)=.34$, ns.). In sum, in the active condition, both categorical and featural similarity governed interference, while in the passive condition, there was only a categorical

influence. These results were unexpected but are informative. First, they suggest that the categorical and featural effects have distinct origins and second, it suggests that some aspect of intentional writing movements underlie the featural effect. We should note that it is possible the lack of a featural effect in the passive condition could be due to proprioceptive noise added by the apparatus and which could render the specific features less distinctive.

An additional conclusion emerges from this experiment: verbal rehearsal of the letters is probably not contributing to the interference effects we observed. This conclusion is based on the assumption that in the passive condition, participants were not rehearsing the letters because they did not know what the items were. Although participants reported not knowing what they were writing, it is still possible that they did know and were unaware of some degree of verbal rehearsal in this condition. This account seems relatively implausible, as it requires unconscious verbal rehearsal of items whose identity the participants claim not to know and under conditions where rehearsal would not be beneficial to performance. In addition, when we analyse the types of errors that participants committed they were never an intrusion from the written stimulus, which would be expected if they were verbally rehearsing the written letters. Errors were almost all from visually similar letters 90% many of which were in the stimulus set (eg. F for H and U for O): 80% of the 90%. The remaining 10% of errors were from other, visually dissimilar, letters.

General Discussion

In a series of studies we have begun to characterize how action interacts with perception during object recognition. Here we look at recognition of objects with which we have extensive experience. Further, this experience is multi-sensory and sensory-motor: letters are seen, written, typed, read and heard. We found that writing interferes with letter perception in an interfering manner: letter perception was worse during concurrent writing. We also found that writing did not interfere with shape perception: therefore, the interference effect was stimulus specific. We assume here that this specificity is due to our experience writing letters. Interference was modulated both by stimulus category and by perceptual similarity, and these two contributions were dissociated in Experiment 4. The categorical effect was obtained in both active and passive conditions, while interference was constrained by featural similarity only in the active condition. Our finding of category-specific interference in a passive condition where no motor commands were required suggests a potential role of proprioception in our effects. The role of proprioceptive feedback on movement execution is controversial (Pipereit, Bock, & Vercher, 2006), as motor movements can be performed without sensory feedback (Christiansen et al., 2007). However, proprioceptive feedback is generally compared with motor commands after a movement, to verify the quality of execution. Whether the proprioceptive feedback in our passive condition may have re-activated previously stored motor commands is unknown, but this leaves open the possibility that interference arose from motor stages even in the passive condition. While prior fMRI work reported motor areas engaged during letter perception (James & Gauthier, 2006; Longcamp et al., 2005, 2006), the studies were motivated by a search

for motor-visual interactions and did not target the distributed network of cortical and subcortical areas that has been involved in proprioception (Kavounoudias et al., 2008). The present findings would motivate further investigation in disentangling the respective influences of motor commands and proprioception in the perception of letters.

Our results add to the growing body of literature on the intimate relationship among the visual and motor systems reflected by action-perception interactions. Here, we find evidence consistent with the idea that motor activity occurring during letter perception (James & Gauthier, 2006) is not epiphenomenal but has a functional role in the visual perception of letters. This relationship between writing and letter perception appears to depend on experience, as we find little evidence for the same link between shape perception and drawing. Unlike many stimuli used in other studies such as tools or kitchen utensils (Chao & Martin, 2000; Grezes & Decety, 2002), letters do not, in themselves, suggest a specific motor act. The relationship between a movement and the visual perception of a letter is learned through extensive experience. Previous work has shown that writing practice can facilitate later visual recognition (Bartolomeo et al., 2002; Longcamp et al., 2005) and here we unravel the opposite side of the equation: the systems are so closely linked that they can interfere with one another if the movement and the perception do not exactly match.

It has been shown that our knowledge of how letters are written influences the way in which they are perceived (eg. Freyd, 1983; Knoblich et al., 2002; Knoblich, 2008; Orliaguet et al., 1997; Tse & Cavanagh, 2000). Our results suggest that the relationship between writing and reading goes beyond stored knowledge and can have an online influence. This is consistent with the idea of a multimodal representation for letters,

reminiscent of Barsalou's theory of perceptual symbol systems (Barsalou, Simmons, Barbey, & Wilson, 2003). Our result can also be interpreted in light of the "common-coding" hypothesis. In this framework, "event codes" and "action codes" share the same representation, allowing for interference (Prinz, 1997). Here, we further specify in what ways the action and the percept must resemble each other to access the same representation and produce interference. Previous work has documented that interference can occur when action is produced concurrently with perception. We show that the magnitude of the interaction between action and perception depends on A) whether the stimuli are from an over-learned category, B) whether the stimuli share perceptual features and C) whether the movements are intentional.

References

- Babcock, M. K., & Freyd, J. J. (1988). Perception of dynamic information on static form. *American Journal of Psychology, 101*, 111-131.
- Barsalou, L. W., Simmons, W. K., Barbey, A. K., & Wilson, C. D. (2003). Grounding conceptual knowledge in modality-specific systems. *Trends in Cognitive Sciences, 7*, 84-91.
- Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences, 22*, 577-660.
- Bartolomeo, P., Bachoud-Levi, A-C., Chokron, S., & Degos, J. D. (2002). Visually- and motor- based knowledge of letters: Evidence from a pure alexic patient. *Neuropsychologia, 40*, 1363-1371.
- Blakemore, S.J., Wolpert, D.M. & Frith, C.D. (2000). Why can't you tickle yourself? *Neuroreport, 11*, 11, 11-15.
- Casile, A., & Giese, M. A. (2006). Non-visual motor learning influences the recognition of biological motion. *Current Biology, 16*, 69-74.
- Chao, L. L., & Martin, A. (2000). Representation of man-made objects in the dorsal stream. *Neuroimage, 12*, 478-484.
- Christensen, M. S., Lundbye-Jensen, J., Geertsen, S. S., Petersen, T. H., Paulson, O. B., & Nielsen, J. B. (2007). Premotor cortex modulates somatosensory cortex during voluntary movements without proprioceptive feedback. *Nature Neurosciences, 10*, 417-419.

- Clark, A. (1998). Embodiment and the philosophy of mind. In A. O'Hear (Ed.), *Current issues in philosophy of mind: Royal Institute Of Philosophy supplement 43* (pp. 35-52). Cambridge, UK: Cambridge University Press.
- Craighero, L., Fadiga, G., Rizzolatti, G., & Umiltà, C. A. (1998). Visuomotor priming. *Visual Cognition, 5*, 109-125.
- Cunningham, A. E., & Stanovich, K. E. (1990). Early spelling acquisition: Writing beats the computer. *Journal of Educational Psychology, 82*, 159–162.
- Decety, J., & Grezes, J. (1999). Neural mechanisms subserving the perception of human actions. *Trends in Cognitive Science, 3*, 172-178.
- Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science, 293*, 2470-2473.
- Ellis, R., & Tucker, M. (2001). Micro-affordance: The potentiation of components of action by seen objects. *British Journal of Psychology, 91*, 451-471.
- Freyd, J. J. (1983). Representing the dynamics of static form. *Memory and Cognition, 11*, 342-346.
- Gallistel, C. R. (1990). *The organization of learning*. Cambridge, MA: MIT press.
- Gauthier, I., Hayward, W. G., & Tarr, M. J. (2002). BOLD activity during mental rotation and viewpoint-dependent object recognition. *Neuron, 34*, 161-171.
- Gerlach, C., Law, I., Gade, A., & Paulson, O. B. (2002). The role of action knowledge in the comprehension of artifacts – A PET study. *Neuroimage, 18*, 928-937.
- Gibson, E.J. (1969). Exploratory behavior in the development of perceiving, acting, and the acquiring of knowledge. *Annual Reviews in Psychology, 39*, 1-41.
- Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston, MA: Houghton Mifflin.

- Grezes, J., & Decety, J. (2002). Does visual perception of object afford action? Evidence from a neuroimaging study. *Neuropsychologia*, *40*, 212-222.
- Grossman, E., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., et al. (2000). Brain areas involved in perception of biological motion. *Journal of Cognitive Neuroscience*, *12*, 711-720.
- Haggard, P., Aschersleben, G., Gehrke, J., & Prinz, W. (2002). Action, binding and awareness. In W. Prinz, & B. Hommel (Eds.), *Common mechanisms in perception and action: Vol. XIX. Attention and performance* (pp. 266-285). Oxford, UK: Oxford University Press.
- Haggard, P., & Clark, S. (2003). Intentional action: Conscious experience and neural prediction. *Consciousness and Cognition*, *12*, 695-707.
- Hamilton, A., Wolpert, D., & Frith, U. (2004). Your own action influences how you perceive another person's action. *Current Biology*, *14*, 493-498.
- Harman, K. L., Humphrey, G. K., & Goodale, M. A. (1999). Active manual control of object views facilitates visual recognition. *Current Biology*, *9*, 1315-1318.
- Hecht, H., Vogt, S., & Prinz, W. (2001). Motor learning enhances perceptual judgment: A case for action-perception transfer. *Psychological Research*, *65*, 3-14.
- Held, R. (1965). Plasticity in sensory-motor systems. Scientific American, *213*(5), 84-89.
- Held, R., & Freedman, S. J. (1963). Plasticity in human sensorimotor control. Science, *142*, 455-462.
- Held, R., & Hein, S. (1963). Movement-produced stimulation in the development of visually guided behavior. J Comp Physiological Psychology, *56*, 872-876.

- James, K. H. (in press). Sensori-motor experience leads to changes in visual processing in the developing brain. *Developmental Science*.
- James, K. H., & Atwood, T. P. (2008). The role of sensori-motor learning in the perception of letter-like forms: Tracking the causes of neural specialization for letters. *Cognitive Neuropsychology*.
- James, K. H., & Gauthier, I. (2006). Letter processing automatically recruits a sensory-motor brain network. *Neuropsychologia*, *44*, 2937-2949.
- James, K. H., Humphrey, G. K., & Goodale, M. A. (2001). Manipulating and recognizing visual objects: Where the action is. *Canadian Journal of Experimental Psychology*, *55*, 111-120.
- James, K. H., Humphrey, G. K., Vilis, T., Corrie, B., Baddour, R., & Goodale, M. A. (2002). "Active" and "passive" learning of three-dimensional object structure within an immersive virtual reality environment. *Behavior Research Methods, Instruments & Computers*, *34*, 383-390.
- James, K. H., James, T. W., Jobard, G., Wong, A. C-N., & Gauthier, I. (2005). Letter processing in the visual system: Different activation patterns for single letters and strings. *Cognitive, Affective and Behavioral Neuroscience*, *5*, 452-466.
- James, T. W., & Gauthier, I. (2003). Auditory and action semantic feature types activate sensory-specific perceptual brain regions. *Current Biology*, *13*, 1792-1796.
- James, W. (1890). *The principles of psychology*. New York: Holt.
- Johnson, M. (1987). *The body in the mind: The bodily basis of meaning, imagination, and reason*. Chicago, IL: University of Chicago Press.
- Kahnmann, D. (1973). *Attention and effort*. New Jersey: Prentice-Hall.

- Kandel, S., Orliaguet, J-P., & Viviani., P. (2000). Perceptual anticipation in handwriting: The role of implicit motor competence. *Perception & Psychophysics*, *62*, 706-716.
- Knoblich, G. (2008). Motor contributions to action perception. In R. Klatzky, B., MacWhinney, B & Behrmann, M., (Eds.). *Embodiment, Ego-Space and Action*. Psychology Press, NY NY.
- Knoblich, G., & Prinz, W. (2001). Recognition of self-generated actions from kinematic displays of drawing. *Journal of Experimental Psychology: Human Perception and Performance*, *27*, 456-465.
- Knoblich, G., Seigerschmidt, E., Flach, R., & Prinz, W. (2002). Authorship effects in the prediction of handwriting strokes: Evidence for action simulation during action perception. *Quarterly Journal of Experimental Psychology*, *55*, 1027-1046.
- Koch, I., & Prinz, W. (2005). Response preparation and code overlap in dual-tasks. *Memory & Cognition*, *33*, 1085-1095.
- Longcamp, M., Anton, J. L., Roth, M., & Velay, J. L. (2003). Visual presentation of single letters activates a premotor area involved in writing. *NeuroImage*, *19*, 1492-1500.
- Longcamp, M., Anton, J. L., Roth, M., & Velay, J. L. (2005). Premotor activations in response to visually presented single letters depend on the hand used to write: A study on left-handers. *Neuropsychologia*, *43*, 1801-1809.
- Longcamp, M., Tanskanen, T., & Hari, R. (2006). The imprint of action: Motor cortex involvement in visual perception of handwritten letters. *NeuroImage*, *33*, 681-688.

- Longcamp, M., Zerbato-Poudou, M., & Velay, J. L. (2005). The influence of writing practice on letter recognition in preschool children: A comparison between handwriting and typing. *Acta Psychologica*, 119, 67-79.
- Lotze, H. (1852). *Medicinische psychologie oder physiologie der seele [Medical psychology or physiology of the mind]*. Leipzig, Germany: Weidmann.
- Lungarely, M., Pegors, T., Bullwinkle, D., & Sporns, O. (2005). Methods for quantifying the informational structures of sensory and motor data. *Neuroinformatics*, 3(3), 243-262.
- Lungarella, M., & Sporns, O. (2005). Information self-structuring: Key principle for learning and development. Proceedings of 2005 4th IEEE International Conference on Development and Learning, 25-30
- Lungarella, M., and Sporns, O. (2006). Mapping information flow in sensorimotor networks. *PLoS Comp. Biol.* 2, 1301-1312.
- Mecklinger, A., Gruenewald, C., Besson, M. N., & von Cramon, D.Y. (2002). Separable neuronal circuits for manipulable and non-manipulable objects in working memory. *Cerebral Cortex*, 12, 1115-1123.
- Miall, R.C., Stanley, J. Todhunter, S., Levick, C. Lindo, S. & Miall, J.D. (2006). Performing hand actions assists the visual discrimination of similar hand postures. *Neuropsychologia*, 44, 966-976.
- Milner, D. A., & Goodale, M. A. (1998). *The visual brain in action*. Oxford, UK: Oxford University Press.
- Musseler, J., & Hommel, B. (1997). Blindness to response-compatible stimuli. *Journal of Experimental Psychology: Human Perception and Performance*, 23, 861-872.

- O'Reagan, K.J. and Noe, A. (2001). A sensorimotor account of vision and visual consciousness, *Behavioral and Brain Sciences*, 24,5, 979-980.
- Orliaguet, J-P., Kandel, S., & Bois, L-J. (1997). Visual perception of motor anticipation in cursive handwriting: Influence of spatial and movement information on the perception of forthcoming letters. *Perception*, 26, 905-912.
- Paillard, J., & Brouchon, M. (1968). Active and passive moments in the calibration of position sense. In S.J. Freeman (Ed.), *The neuropsychology of spatially oriented behavior* (pp. 37-55). Homewood, IL: Dorsey Press.
- Park, S., Toole, T., & Lee, S. (1999). Functional roles of the proprioceptive system in the control of goal-directed movement. *Perceptual and Motor Skills*, 88, 631-647.
- Pelli, D. G., Robson, J. G., & Wilkins, A. J. (1988). The design of a new letter chart for measuring contrast sensitivity. *Clinical Vision Sciences*, 2, 187-199.
- Pipereit, K., Bock, O., & Vercher, J-L. (2006). The contribution of proprioceptive feedback to sensorimotor adaptation. *Experimental Brain Research*, 174, 45-52.
- Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive Psychology*, 9, 129-154.
- Reed, C. L., & Farah, M. J. (1995). The psychological reality of the body scheme: A test with normal participants. *Journal of Experimental Psychology: Human Perception and Performance*, 21, 334-343.
- Repp, B. H., & Knoblich, G. (2007). Towards a psychophysics of agency: Detecting gain and loss of control over auditory action effects. *Journal of Experimental Psychology: Human Perception and Performance*, 33, 469-482.

- Rizzolatti, G., Carmada, R., Fogassi, L., Gentilucci, M., Luppino, G., & Matelli, M. (1988). Functional organization of inferior area 6 in the macaque monkey II: Area F5 and the control of distal movements. *Experimental Brain Research*, *71*, 491-507.
- Schubo, A., Aschersleben, G., & Prinz, W. (2001). Interactions between perception and action in a reaction task with overlapping S-R assignments. *Psychological Research*, *65*, 145-157.
- Schutz-Bosbach, S. and Prinz, W. (2007). Perceptual resonance: action-induced modulation of perception. *Trends in Cognitive Sciences*, *11*,8, 349-355.
- Schwartz, D. L. (1999). Physical imagery: Kinematic versus dynamic models. *Cognitive Psychology*, *38*, 433-464.
- Schwartz, D. L., & Holton, D. L. (2000). Tool use and the effect of action on the imagination. *Journal of Experimental Psychology: Learning, Memory and Cognition*, *26*, 1655-1665.
- Seki, K., Yajima, M., & Sugishita, M. (1995). The efficacy of kinesthetic reading treatment for pure alexia. *Neuropsychologia*, *33*, 595-609.
- Sternberg, S. (2001). Separate modifiability, mental modules, and the use of pure and composite measures to reveal them. *Acta Psychologica*, *106*, 147-246.
- Tse, P. E., & Cavanagh, P. (2000). Chinese and Americans see opposite apparent motions in a Chinese character. *Cognition*, *74*, B27-B32.
- Tucker, M., & Ellis, R. (2001). The potentiation of grasp during visual object categorization. *Visual Cognition*, *8*, 769-800.

- Valyear, K. F., Culham, J. C., Sharif, N., Westwood, D. A., & Goodale, M. A. (2006). A double dissociation between sensitivity to changes in object identity and orientation in the ventral and dorsal visual streams: A human fMRI study. *Neuropsychologia, 44*, 218-228.
- van Atteveldt, N., Formisano, E., Goebel, R., & Blomert, L. (2004). Integration of letters and speech sounds in the human brain. *Neuron, 43*, 271-282.
- Wexler, M., Kosslyn, S. M., & Berthoz, A. (1998). Motor processes in mental rotation. *Cognition, 68*, 77-94.
- Wexler, M., & van Boxtel, J. J. A. (2005). Depth perception by the active observer. *Trends in Cognitive Science, 9*, 431-438.
- Wilson, M. (2002). Six views of embodied cognition. *Psychonomic Bulletin and Review, 9*, 625-636.
- Wolpert, D.M., Ghahramani, Z. & Jordan, M.I. (1995). An internal model for sensorimotor integration. *Science, 269*, 1880-1882.
- Wong, Y. K., & Gauthier, I. (submitted). A multimodal neural network recruited by expertise with musical notation.
- Zatorre, R. J., Chen, J. L., & Penhune, V. B. (2007). When the brain plays music: Auditory-motor interactions in music perception and performance. *Nature review: Neuroscience, 8*, 547-558.

Figure Captions

Figure 1:

- a. Example of stimuli used in Experiments 1-4. Top row: letters presented just above psychophysical threshold, bottom row: shapes presented just above threshold.
- b. Schematic of interference paradigm: Participant looked at computer screen to identify letters or shapes verbally while writing letters or shapes concurrently.

Figure 2:

Amount of interference plotted as a function of letter seen in Experiment 1. In this, and all graphs, error bars are 95% confidence intervals of the comparison with zero.

Figure 3:

Amount of interference plotted as a function of letter seen in Experiment 2.

Figure 4:

Amount of interference of writing on straight letter perception in Experiment 2. Note here that the X-axis depicts the stimulus written. All stimuli written interfered significantly with stimuli seen, but the amount differed depending on category and curvature.

Figure 5:

- a) Amount of interference plotted as a function of letter seen in Experiment 3.
- b) Amount of interference plotted as a function of shape seen in Experiment 3.

Figure 6:

Amount of interference of writing on straight letter perception in Experiment 3.

Figure 7:

Schematic of the apparatus used in Experiment 4. The experimenter (left) and the participant (right) were separated by a black curtain. The experimenter wrote or drew the stimulus presented to her, which moved the yoking apparatus, moving the participants hand in the same

manner. The participant's hand was placed into a neoprene glove and rested on a small platform, allowing them to relax the hand completely. During the passive condition, the participants relaxed their hand, such that it was moved only by the experimenter. In the active condition, the participant moved their own hand.

Figure 8:

a) Amount of interference plotted as a function of letter seen in the active condition in Experiment 4.

b) Amount of interference plotted as a function of letter seen in the passive condition in Experiment 4.

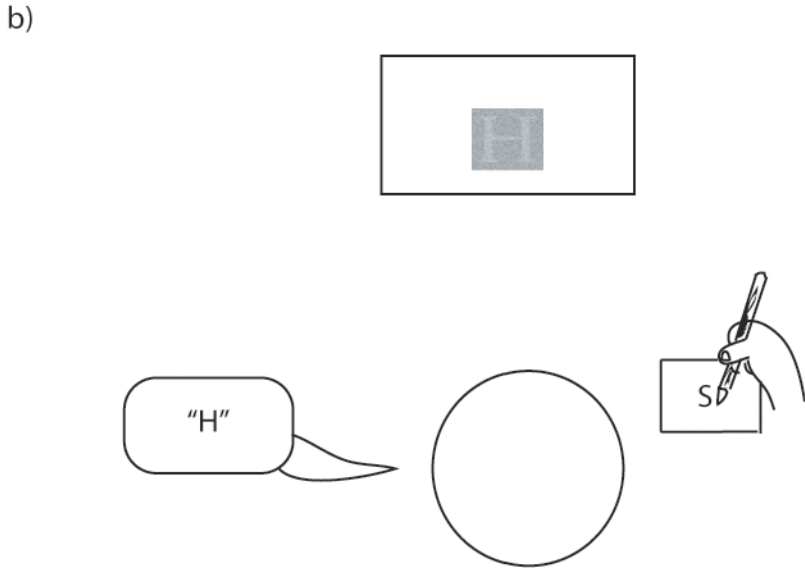
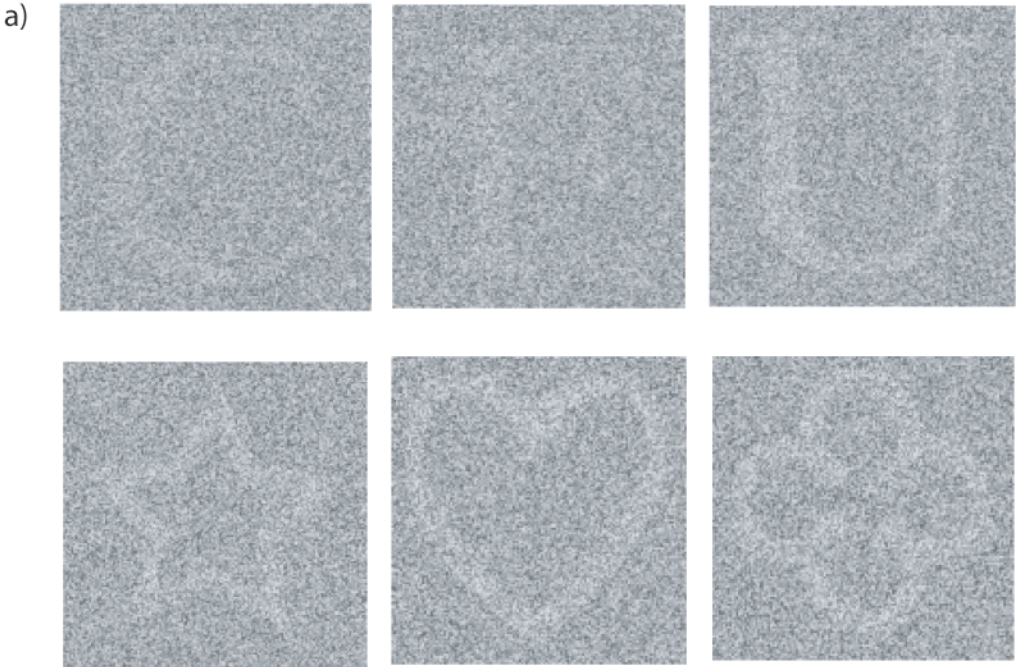
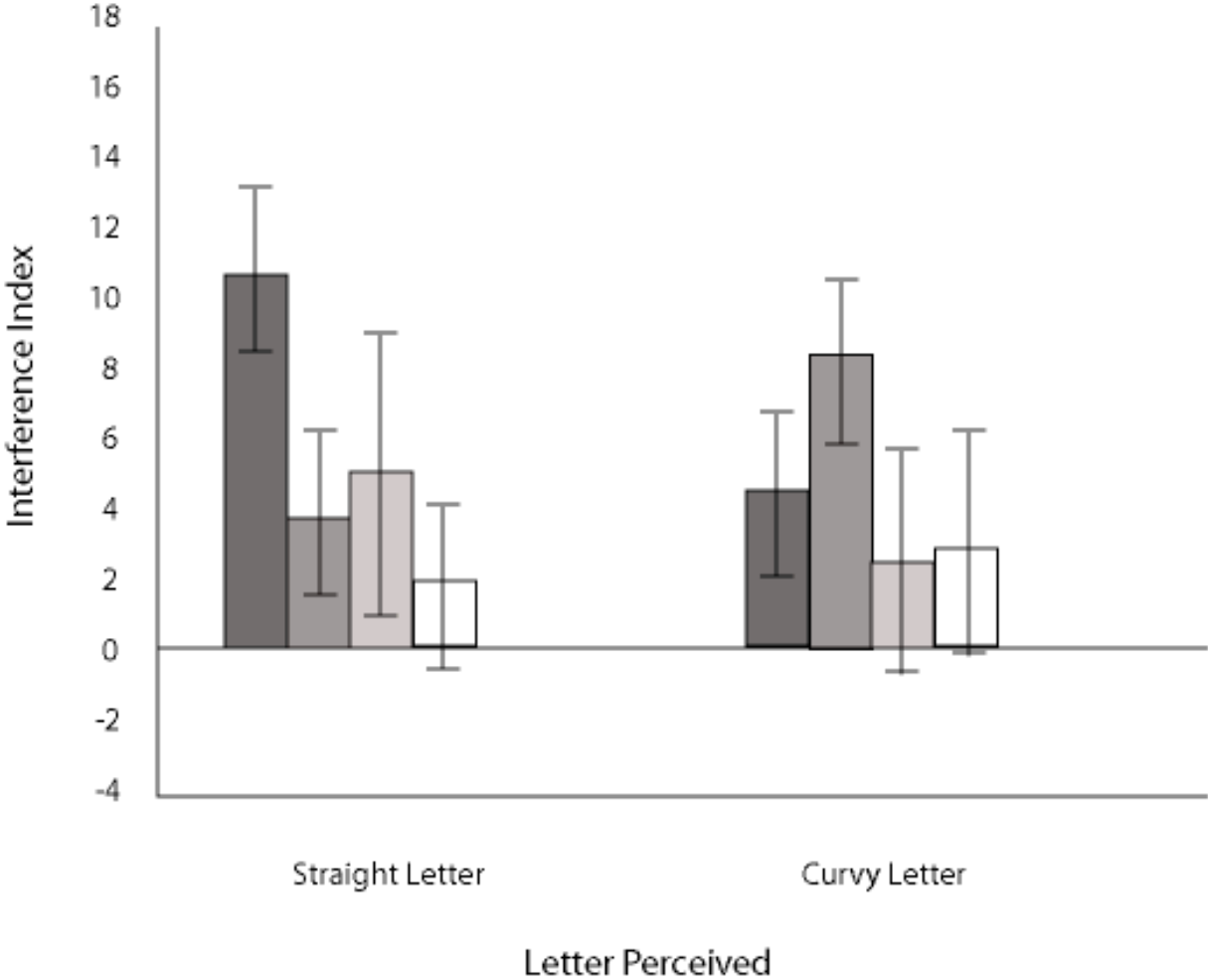


Figure 1



Stimulus written

- straight letter
- curvy letter
- straight shape
- curvy shape

Figure 2

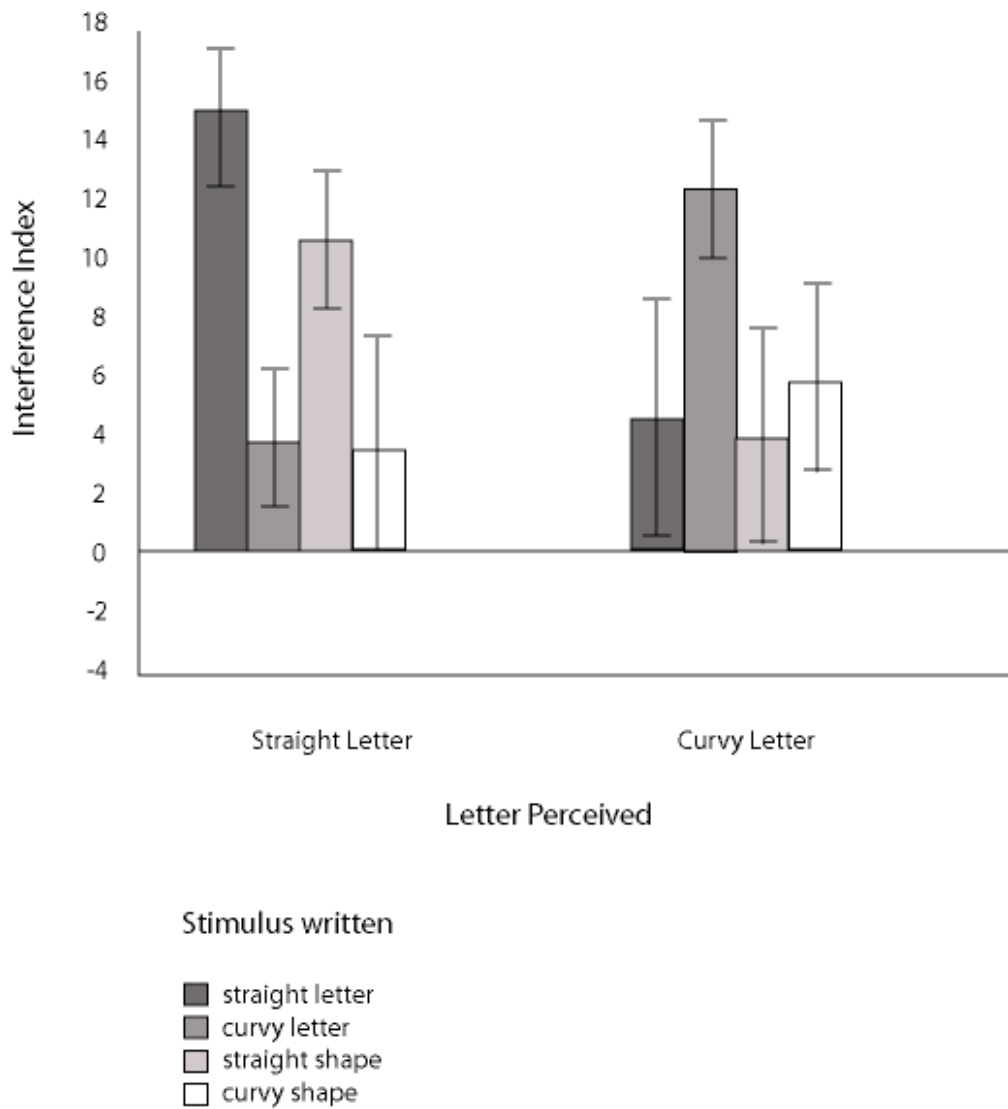


Figure 3

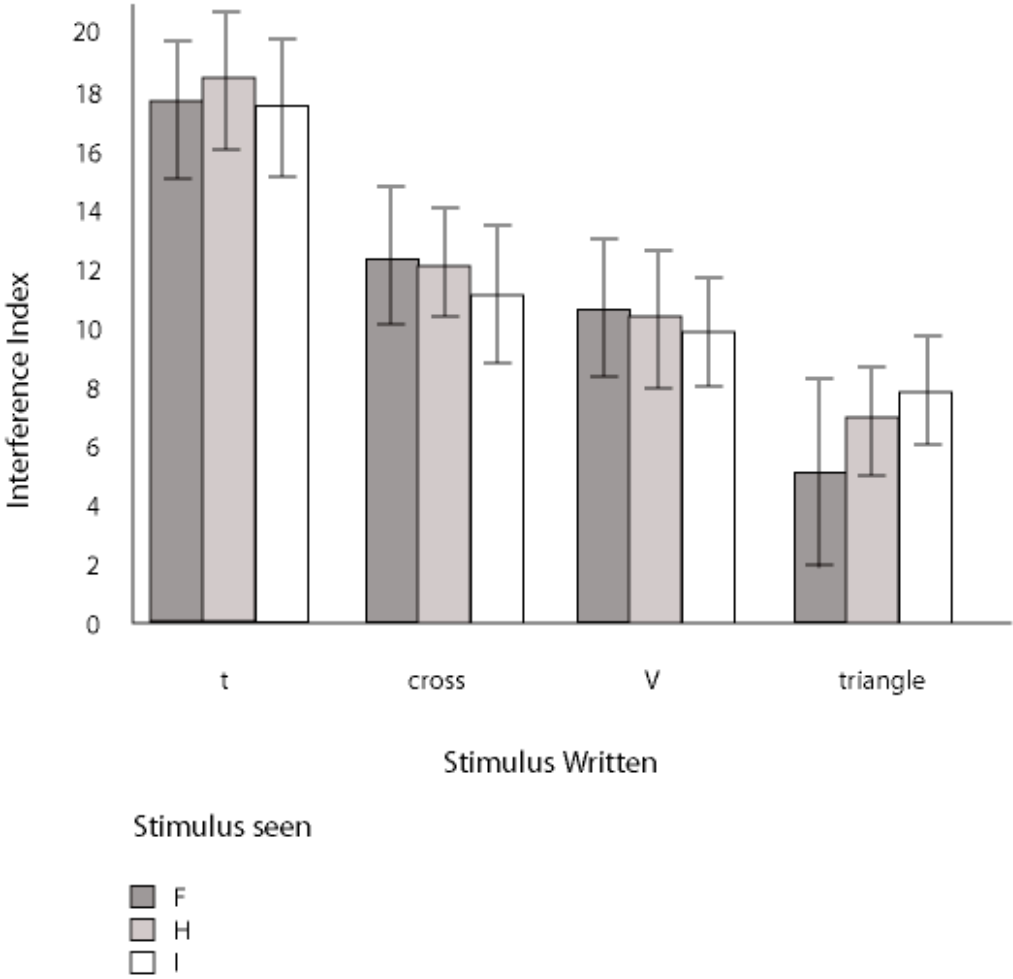
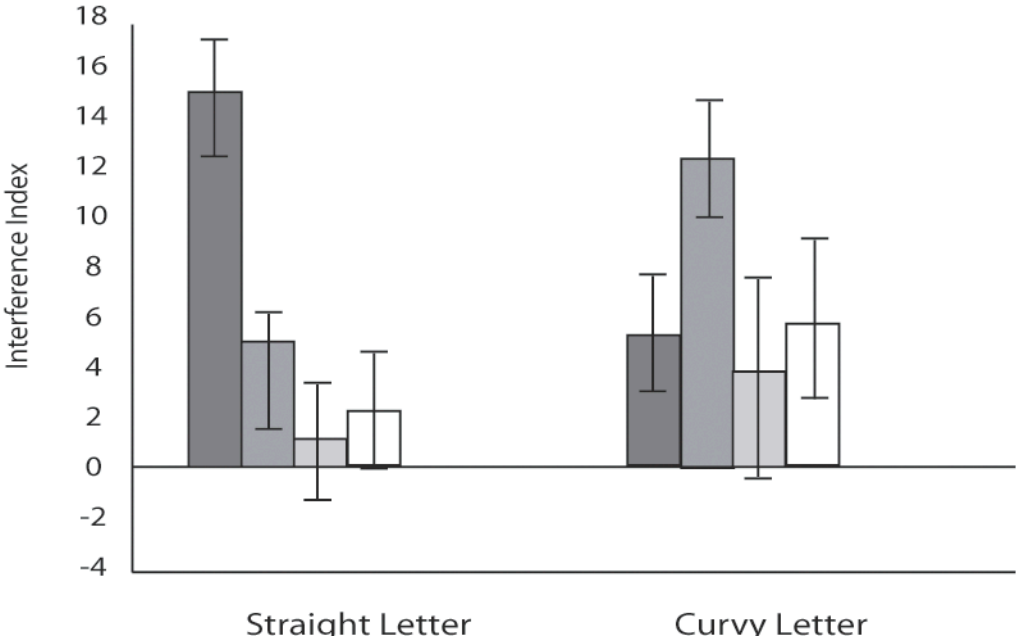
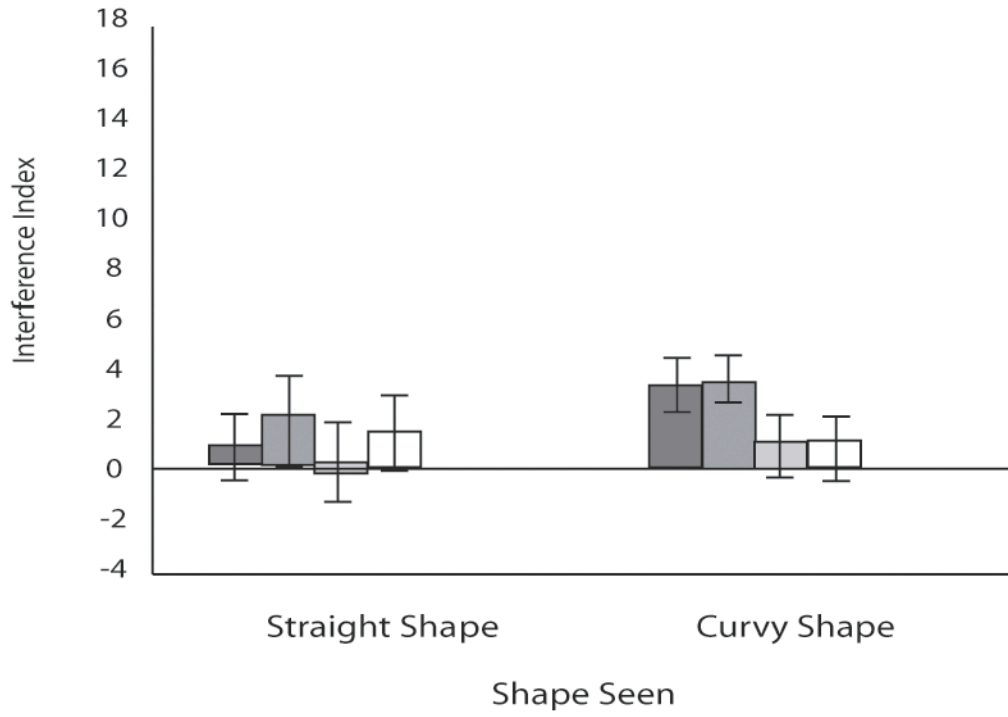


Figure 4

a.



b.



Stimulus written

- straight letter
- curvy letter
- straight shape
- curvy shape

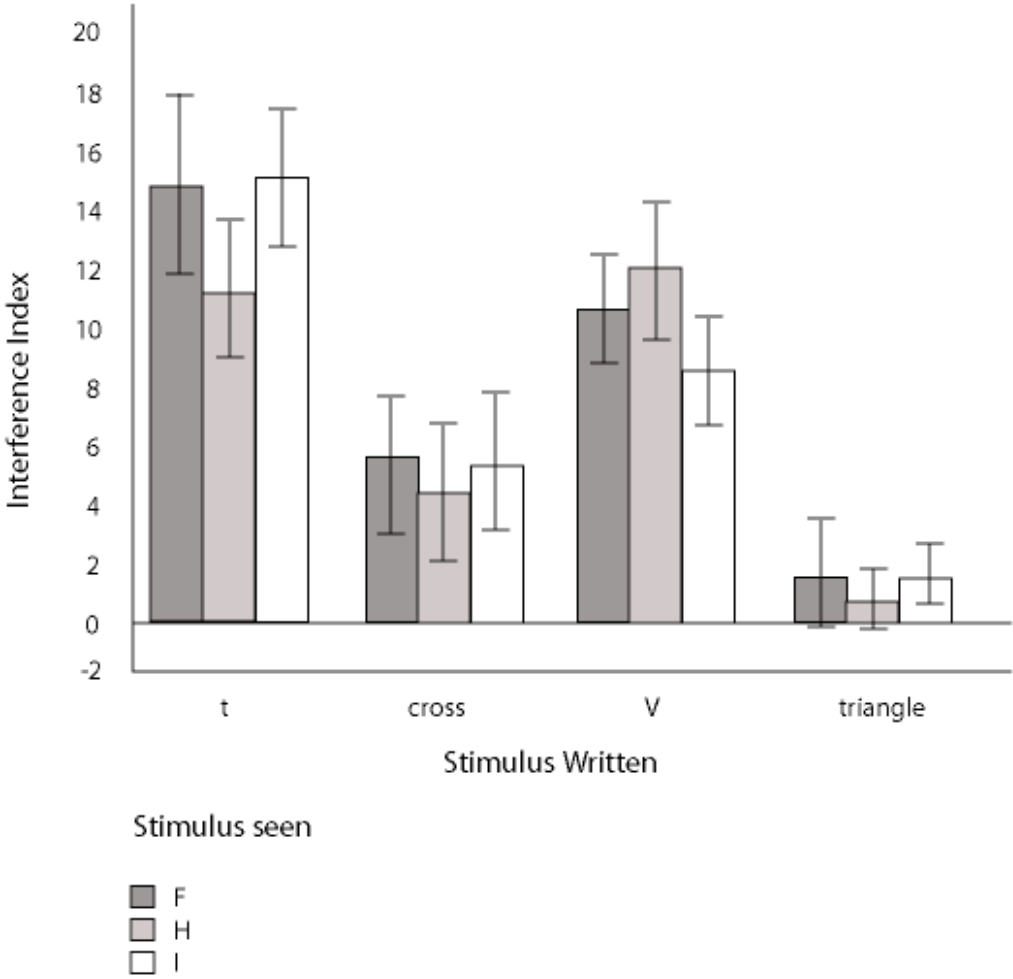


Figure 6

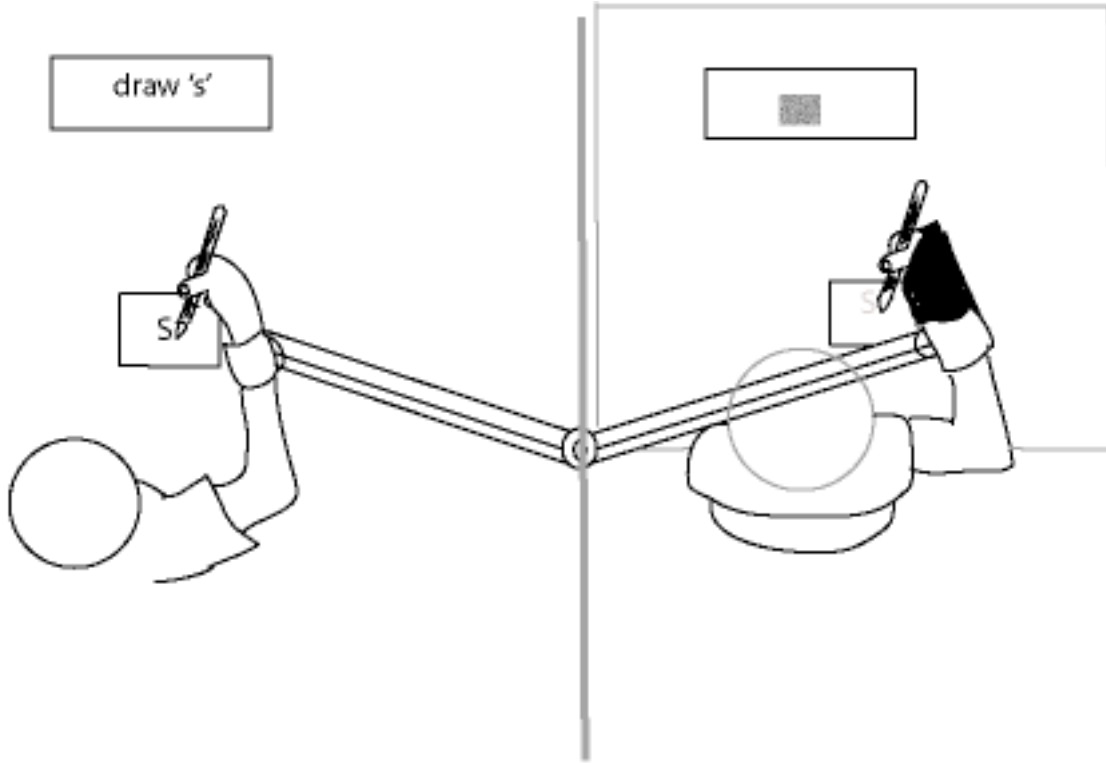


Figure 7

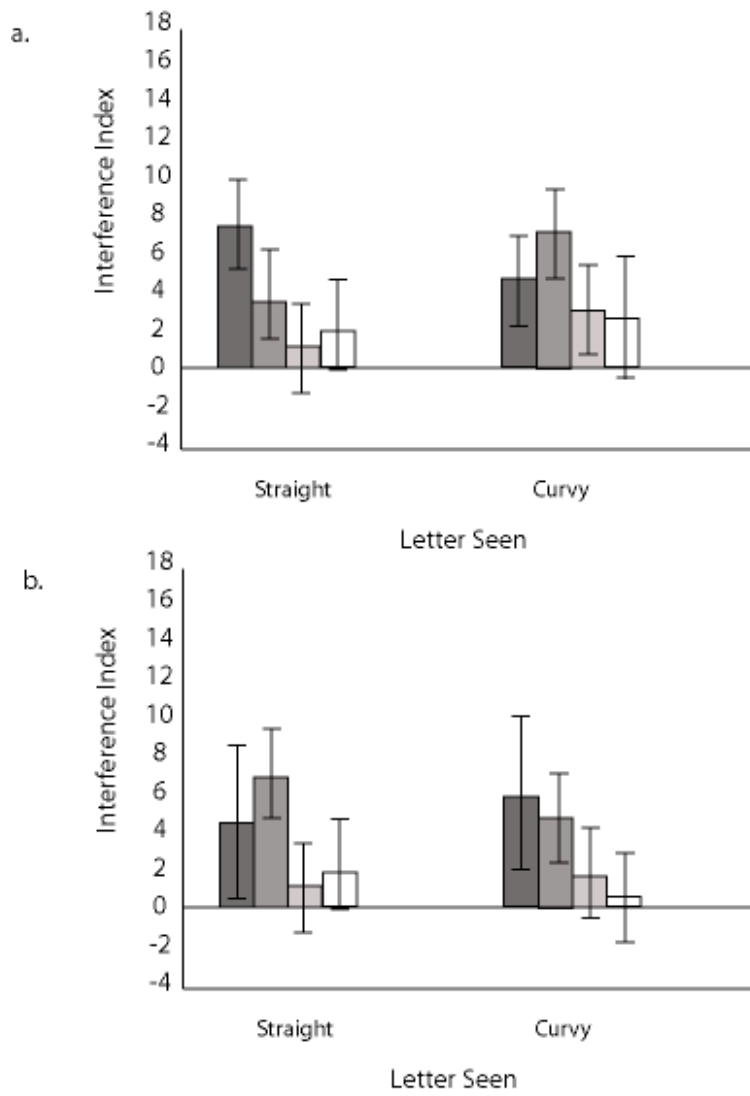


Figure 8

Table Caption:

Mean and standard deviations of all raw scores in the Experiments.

Table 1

Experiment 1

		Baseline	write condition		straight shapes	curvy shapes
			straight letters	curvy letters		
	see condition					
Mean (SE)	Straight letters	77.7 (2.2)	67.5(2.5)	73.7(2.0)	74.1(2.8)	75.9(2.2)
	curvy letters	75 (3.0)	71.6 (2.4)	67.8(2.0)	73.4(2.7)	72.7(2.2)

Experiment 2

		Baseline	write condition		straight shapes	curvy shapes
			straight letters	curvy letters		
	see condition					
Mean (SE)	Straight letters	78.7 (3.2)	63.2(3.5)	74.7(2.1)	68.1(2.2)	74.9(2.3)
	curvy letters	77 (2.4)	73.4 (2.7)	65.8(1.9)	74.4(2.0)	71.3(2.6)

Experiment 3

		Baseline	write condition		straight shapes	curvy shapes
			straight letters	curvy letters		
	see condition					
Mean (SE)	Straight letters	76.7 (2.2)	60.7(2.5)	72.7(2.0)	75.1(1.9)	74.8(2.1)
	curvy letters	75 (2.1)	70.2 (2.0)	63.5(2.2)	72.4(2.2)	69.3(3.1)
	straight shapes	75.0(2.0)	74.0 (1.6)	73(2.7)	75.3(2.9)	73.5(2.9)
	curvy shapes	75.4(2.1)	72.5 (2.0)	72.2(2.5)	74.6(2.7)	74.3(2.4)

Experiment 4

		Baseline	write condition		straight shapes	curvy shapes
			straight letters	curvy letters		
Active	see condition					
Mean (SE)	Straight letters	74.7 (2.7)	67.2(2.1)	71.3(2.6)	73.8(2.4)	72.4(2.6)
	curvy letters	74 (2.8)	70.2 (2.3)	67.5(2.8)	71.4(2.5)	72.1(2.7)
	straight shapes	74.2(2.5)	74.2 (1.6)	74.5(2.2)	74.3(2.0)	74.9(2.7)
	curvy shapes	73.9(2.4)	74.0 (2.2)	73.2(2.3)	73.1(2.0)	73.0(2.1)

write condition

Writing interferes with letter perception

Passive		straight letters	curvy letters	straight shapes	curvy shapes
	see condition				
Mean (SE)	Straight letters	70.7(2.9)	68.7(2.0)	73.1(2.9)	73.8(2.5)
	curvy letters	69.2 (2.6)	70.5(2.3)	72.4(2.5)	73.3(2.1)
	straight shapes	74.0 (2.6)	74.5(2.3)	74.1(1.3)	74.6(1.7)
	curvy shapes	74.3 (1.9)	73.2(2.1)	73.5(1.5)	73.2(2.1)