RESEARCH ARTICLE

Sex differences in the acquisition of complex skilled movements

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Abstract The praxis system comprises a network of brain regions dedicated to complex skilled movements. Following suggestions of a female advantage on learned movements (Chipman and Hampson in Neuropsychologia 44(12):2315–2329, 2006), we investigated how males and females *acquire* skilled movements. Subjects viewed and imitated sequences of hand movements, which were repeated ten times. Subjects' imitations were captured by a data glove, and the temporal and spatial characteristics of the imitations were compared to the model sequence. We propose an account of the computations required for imitating hand movement sequences and define the errors that may arise from failures at these computations. Our results demonstrate a female advantage in the acquisition of hand movement sequences and show that this sex difference is accounted for by a female advantage in planning, rather than an advantage in execution or online control. Further, the female advantage is specific to the production of items within a sequence and does not affect the proper ordering of items. Our findings have important implications for sex-sensitive instructional strategies, as well as for understanding the human praxis system.

Keywords Imitation · Sequence learning · Apraxia · Sex differences · Gesture

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Introduction

Imitation is critically important for learning many new skills. Viewing and imitating hand movements activates a fronto-parietal network of brain regions (Muhlau et al. 2005) that are associated with skilled movements; this left hemisphere dominant system is known as the praxis system. Damage to this system results in a neurological disorder known as ideomotor apraxia (see Heilman and Rothi 2003; Wheaton and Hallett 2007, for review). Patients with ideomotor apraxia lose the temporal and spatial fidelity of skilled movements, which can include gesturing to command, imitating seen movements, as well as pantomimed and actual tool use (Johnson-Frey 2003).

Researchers have identified sex differences in the praxis system's anatomical and functional organization. For example, apraxia more often results from anterior lesions than from posterior lesions in females (Kimura 1983). Moreover, Chipman and Hampson (2006) show that non-apraxic females have an advantage on tasks that depend upon this system. Chipman and Hampson required subjects to produce distinct movements in response to color cues and had judges view video records of subjects' performance. The judges noted that females made fewer perseverations, intrusions and substitutions, and executed their movements faster than males did. The researchers concluded that this female advantage in gesture production arises from a sex difference in the efficiency of motor selection.

Although the study of Chipman and Hampson (2006) provided some insights into sex differences in gesture production, its experimental paradigm and analytic approach are limiting. First, the analysis focused primarily on well-learned movements, so it is unclear whether the female advantage extends to the acquisition of unfamiliar

movements. Knowing this result's extensibility is important for optimizing rehabilitation strategies for apraxia, and also for developing sex-sensitive strategies for teaching motor skills. Moreover, although video recordings of performance are useful, they are not an easy basis for fine-grained, objective analysis of the temporal and spatial components of the movements that are recorded.

The present study utilizes a novel approach, developed by our group (Gold et al. 2008), to clarify the sex differences in the functional organization of the praxis system and to determine whether sex differences are evident in the acquisition of complex movements. In the experimental paradigm, subjects view, and then reproduce from memory, a stimulus model comprising a sequence of hand gestures. The subjects' movements are captured by a data glove and then analyzed with a multi-stage algorithm that identifies spatial and temporal differences between the stimulus model's movement and the subject's imitation. The algorithm isolates errors not only for particular items in a sequence but also for the order in which the items are reproduced; this distinction between the two types of errors is important as separate brain regions contribute to memory for item and order information (Histed and Miller 2006). Our stimuli comprise movements of the digits, with the hand position and orientation held constant. While previous research has shown that apraxia affects hand movements more than finger movements, left hemisphere damage impairs both types of movements (Goldenberg 1999). In addition, recent fMRI research in healthy subjects has shown that there are no differences in the neuroanatomical correlates of finger and hand gesture imitations (Muhlau et al. 2005).

Our experimental paradigm has the added advantage of allowing control over visual feedback. In particular, we are able to yoke a subject's movements in real time to the movements of an animated hand displayed on a computer monitor. On a trial-by-trial basis, we could present this feedback to subjects, or turn it off. This manipulation is important to our investigation as it has been demonstrated that males show greater reliance on visual feedback than females on praxis tasks (Chipman et al. 2002). Also, some research has shown that apraxia is associated with an increased reliance on vision (Heilman et al. 1986; Ietswaart et al. 2006).

Our experimental task depends on a series of distinct cognitive processes. Figure 1 summarizes our proposed model of these processes and identifies the distinctive types of errors that likely would arise from failures of each. For simplicity's sake, the diagram portrays the processes as being serially ordered, but it is entirely possible that portions of some of the processes actually operate in parallel. The diagram is presented here in order to guide the reader

through the rationale for our analysis and the interpretation of error types.

It should be noted that our experimental task only assesses sequence production. It is possible, however, that errors in sequence production actually arise earlier, during sequence encoding, including the perception of the sequence or memory encoding. To rule out the possibility that any sex-dependent differences arise from failures at the level of perception or encoding, we carried out an additional task where males and females watched a sequence of movements, followed by a computer-generated attempted imitation of the sequence. The subjects were required to rate the fidelity of the imitation. Note that this task involves the same stimuli as our gesture production task and requires sequence perception and encoding, without sequence production.

Our study attempts to refine the characterization of previously reported sex differences on a task that draws heavily on the fronto-parietal praxis network (Muhlau et al. 2005). The study has several objectives: (1) to confirm the previously reported female advantage on gesture production; (2) to identify those computations that females perform more efficiently than males do; (3) to determine whether the female advantage is restricted to well-learned skilled movements or whether such an advantage is evident during the acquisition of such sequences; and (4) to examine sex differences in the exploitation of visual feedback during the course of learning.

Experiment 1

Method

Subjects

Twenty-six subjects were recruited from the Brandeis University community, eight of these subjects (four female, four male) were excluded from the analysis due to technical problems during testing. Of the eighteen subjects included in the analysis, there were nine males (mean = 23.89 years old, SD = 6.95) and nine females (mean = 21 years old, SD = 4.15). Each subject gave written informed consent in accordance with the principles of the Declaration of Helsinki, and the protocol had been approved by Brandeis University's Committee for the Protection of Human Subjects. All subjects had normal or corrected-to-normal vision and were right-handed (Oldfield 1971). All subjects reported no prior experience with American Sign Language (ASL), which is important because some of our stimuli were similar to letters in ASL's finger spelling alphabet.
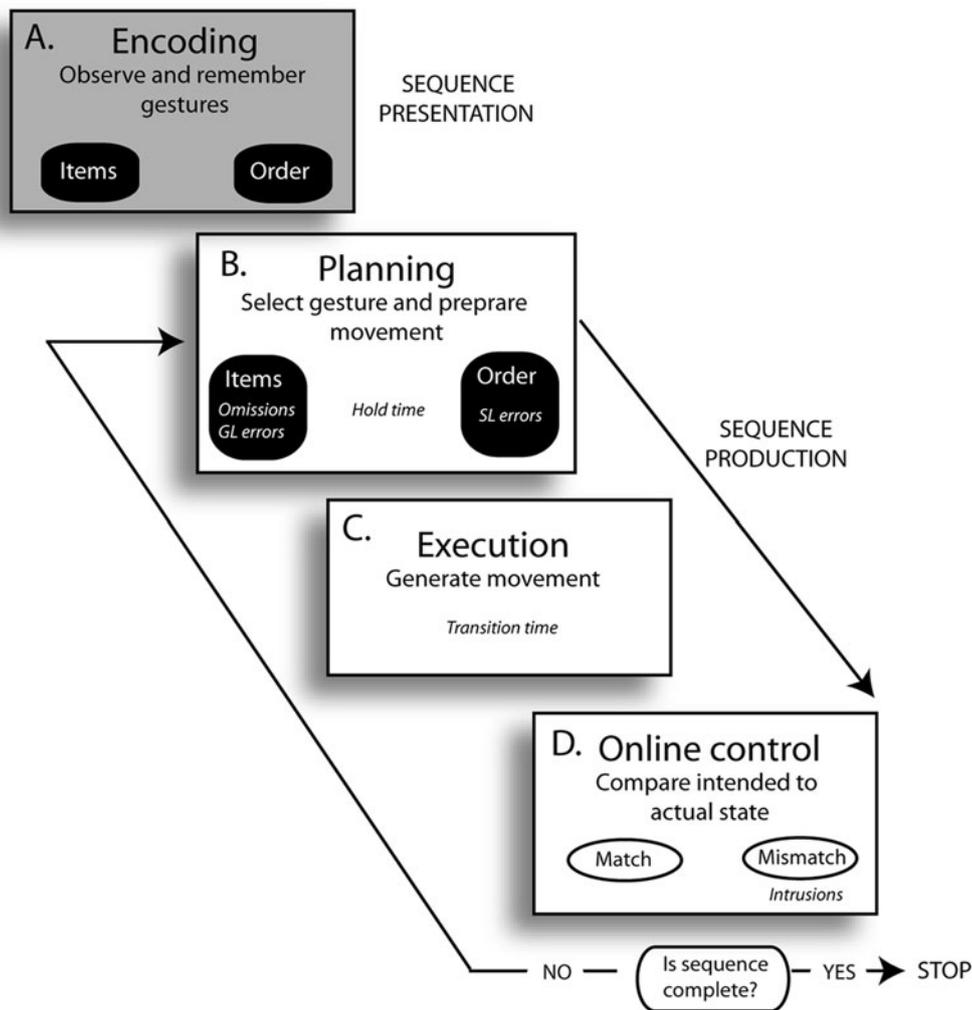
Fig. 1 Key processes involved in reproducing a sequence of just-seen hand gestures. Each process is associated with one or more dependent variables (identified in *italics*). *A* The sequence of gestures is encoded during viewing. The information extracted includes the identity of individual gestures (item information) and the place in the sequence that it occupied (order information). *B* Using both item and order information, a motor plan is developed, which involves selecting a gesture for production and preparing to make the movement. An omission of a gesture reflects a failure to reproduce an item, whereas Gesture-Level (GL) errors reflect the reproduction of an incorrect item. Sequence-Level (SL) errors occur when items are produced in the wrong order. A motor command must be generated to transition from the current gesture to the next one. Although an individual item could appear in more than one sequence, the gesture immediately preceding and following a particular gesture would not occur in another sequence. Thus, the motor commands to transition from one gesture to the next were novel in each of the different sequences. The process of generating a motor command is reflected in the hold time, i.e., how long a gesture is maintained before the transition to the next one is initiated. *C* The gesture is produced by changing fingers' flexions and extensions from their current state to the state required for the new gesture. This process is reflected in transition time, i.e., the time required to change from the current gesture to the new one. *D* To ensure accuracy of reproduction, the movement must be monitored and corrected if necessary. This involves a comparison between the current state and the selected state. If a match is detected, one will move onto the next item in the sequence, if a mismatch is detected, subjects will correct the movement, which can be observed in intrusions. This series of computations will continue to be executed until the entire sequence is completed

Stimuli

The details of the method used to generate model gesture sequences have been described elsewhere (Gold et al. 2008). Model sequences were generated from 16 hand gestures, each defined by its combination of extensions and flexions of the five digits on the right hand.

Experimental model sequences comprised eight different sequences of six gestures. Within any sequence, from one gesture to the next, two digits changed flexion/extension (Fig. 2). Each pair of successive gestures appeared just once across all sequences. Single, static gestures and two-gesture sequences served as practice stimuli.

Fig. 2 Illustration of the events that define the stimulus-presentation phase of an experimental trial. Sequences of six different hand gestures are displayed on a screen, bookended by gestures in which all the digits of the hand are extended, signaling the start and end of the sequence. Each gesture is shown in static form for 1 s. Successive static gestures are separated by a 500-ms transition period during which subjects see a smooth transition that morphs one gesture into another. The total time to complete a model sequence is 11.5 s. Note that the stimuli were presented in Caucasian flesh color during the experiment, rather than in the gray scale depicted here
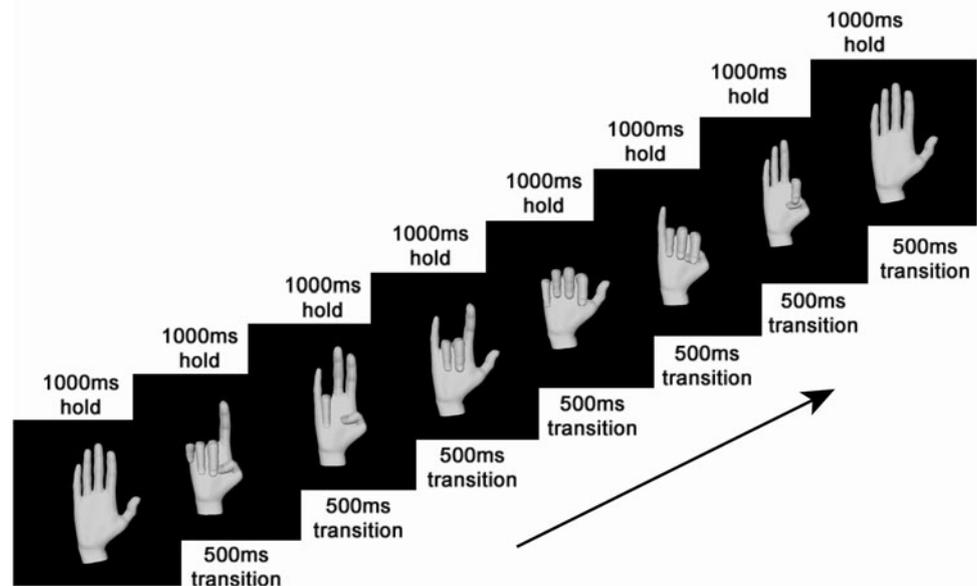
Apparatus

Subjects performed each imitation while wearing a right-handed 5DT^{TM} DataGlove (Fifth Dimension Technologies) and hand and wrist sensors from a Polhemus (Patriot^{TM}) motion tracking system (for further details see Gold et al. 2008).

A wooden frame with a curtain (positioned in line with the shoulder) occluded subjects' vision of their right hand and arm throughout the experiment. However, on some trials, subjects viewed a real-time animation of their hand movements using Vizard^{TM} VR Toolkit (WorldViz). The hand animation looked identical to the hand viewed during the stimulus presentation; however, each of the digits as well as the position and orientation of the hand and wrist was electronically yoked to the subject's fingers, hand and wrist, and moved ($\sim$30 ms delay) with the subject's own movements.

Procedure

Subjects viewed and imitated the stimuli seated at a table, with their right elbow supported on a foam rest, with the palm of the hand facing the shoulder and the fingers extended. This orientation allowed subjects to imitate sequences without having to mentally rotate the stimulus. In the first set of trials, subjects viewed one static gesture at a time, and when a tone sounded, they imitated the gesture. Each of the 16 gestures was displayed for 1 s, with a 1-s retention delay before the tone. Next, subjects practiced with sequences comprising two gestures, with a 1-s retention delay before being cued to imitate the sequence. After viewing and reproducing eight different two-item practice sequences, subjects went onto the experimental phase of

the experiment. In all practice trials, visual feedback of the subject's hand was provided.

In the experiment proper, subjects were told that they would see six-item sequences of gestures, which they should imitate when the auditory "go" signal was given. They were told to produce as many of the gestures as they could remember, and to produce the gestures in the correct order, while refraining from guessing. They were informed that they would learn four different six-item sequences, and they would see each of the sequences repeated over ten successive trials. Further, subjects were informed that visual feedback of their hand movements would be visible on the display screen while they were learning two of the sequences but that no visual feedback would be available while they learned the other two sequences. When a condition called for visual feedback, subjects saw on the computer monitor an animation of a hand whose movements were yoked to the movements of the subjects' hand. When a condition called for no visual feedback, subjects viewed a blank display as they reproduced each sequence. Subjects were allotted 14 s to complete the imitation and used the left hand to initiate the next trial with a key press.

Analysis

A multi-stage algorithm analyzed the flexion/extension captured from the data glove and compared the subjects' imitation to that of the model (Gold et al. 2008). The algorithm begins by segmenting each imitation and its corresponding sequence into component gestures. Based on the velocity of each digit's movements, the algorithm segments the sequence into static or transitional components. A gesture qualifies as "static" if the velocity of each

digit drops below 10% of its peak velocity for at least 100 ms; a "transitional" component is defined by the finger movements between two successive static gestures.

Once transitional and static components have been defined, our algorithm examines the flexion data for each digit in each time epoch. The flexion threshold was defined as a value of 0.5, with any digit whose flexion value exceeded that threshold considered to be flexed, and any digit with a flexion value below the threshold considered to be extended. Each gesture can be characterized by its extended digits, starting with the thumb (1) and ending with the little finger (5). Thus, in this notation, a completely open hand, all fingers extended, would be represented as 12345.

Once the component gestures in a sequence have been identified, the algorithm compares the subject's imitation against the model gesture sequence; this comparison gauged the accuracy and timing of each imitation. The "bookend" gestures (i.e., the open-hand gestures at the start and end of each sequence) were discarded from both the model and its reproduction. After comparing each gesture in the imitation to gestures in the model, the algorithm reorders the gestures recovered from the imitation so as to minimize the number of incorrectly reproduced gestures across the entire gesture sequence.

After matching the reproduced gestures against the gestures in the model, the algorithm quantifies and categorizes the spatial and temporal components of the subject's movements, which are described below.

Spatial errors

Omissions

When one or more gestures in the imitation cannot be matched to any gesture in the model sequence. For example, if the model sequence 2–235–125–1–5–345 was reproduced as 2–235–125–1, the algorithm would assert that 5 and 345 had been omitted from the reproduced sequence and would therefore attribute two omissions to that trial. Omissions are observed when fewer than six gestures are produced in the subject's reproduction, and as such reflect a failure to select a gesture for response, a component of motor planning (Fig. 1b).

Intrusions

When the number of gestures imitated exceeds the number of gestures in the model sequence. Note that every model sequence comprised six gestures, a fact brought to subjects' attention before the experiment. For example, if the sequence 2–235–125–1–5–345 was reproduced as 2–235–1235–125–1–5–345, the algorithm would find that gesture

1235 was an intrusion, added in the subject's reproduction, and as such mark one intrusion for that trial. Intrusions likely reflect a corrective response, in this case 1235 was an incorrect response and was corrected to the appropriate gesture 125. Corrective responses are part of online control processes (Fig. 1d).

Gesture-Level errors

When a reproduced gesture differs from the matched gesture in the model by one or more digit flexions. For example, if the sequence 2–235–125–1–5–345 was reproduced as 2–235–135–1–5–345, the gesture 135 in the subjects' reproduction would be matched to 125 in the model, but one Gesture-Level error would be defined as subjects extended their middle finger instead of their index finger. As Fig. 1b suggests, Gesture-Level (GL) errors reflect the selection of an incorrect gesture, a component of motor planning.

Sequence-Level errors

When gestures are reproduced in the incorrect order. For example, if the sequence 2–235–125–1–5–345 was reproduced as 2–125–235–1–5–345, two Sequence-Level errors would be defined, as gesture 125 was produced second instead of third and 235 was reproduced third instead of second. Note that when the algorithm must re-order gestures in a reproduction in order to find a match in the model sequence, this re-ordering would denote a Sequence-Level error. Also note that intrusions and omissions do not influence our measure of Sequence-Level errors. Sequence-Level errors reflect difficulty in planning items in the correct order (Fig. 1b).

As Gesture-Level errors and Sequence-Level errors become more likely as additional gestures are reproduced per sequence, we normalized the values of these variables to the number of gestures produced per sequence. This is an important normalization as over successive repetitions of a sequence, subjects produce more gestures (1st repetition: mean = 3.22, SEM = 0.28); 10th repetition: mean = 5.69, SEM = 0.18), $(F_{(3.363,53.809)} = 24.701, p < 0.001, \eta_p^2 = 0.607)$. Additionally, males (mean = 4.85, SEM = 0.17) consistently produce fewer gestures than females (mean = 5.36, SEM = 0.15) $(F_{(1,16)} = 5.304, p = 0.035, \eta_p^2 = 0.249)$.

Temporal components

Hold time

The mean time (ms) that a subject holds each of the static gestures. This provides a measure of movement

planning time, as subjects generate a motor command to move from one gesture to the next (Fig. 1b). Note that the value of this variable can be compared to the value of 1,000 ms, which was the time each gesture in a model was held.

Transition time

The mean time (ms) that a subject takes to transition from one gesture to the next. This provides a measure of movement execution time (Fig. 1c). Note that the value of this variable can be compared to the value of 500 ms, which was the transition time from one gesture to the next for the model sequence.

Serial position

As our task entails serial recall, performance is likely to vary with an item's serial position. Thus, we compared each item in the model sequence to the corresponding item in the reproduction. A correct match was assigned a value of 1, and an incorrect match was assigned a 0. For example, if the sequence 2–235–125–1–5–345 was reproduced as 2–235–125–1, the trial would be coded as correct for serial positions one through four, and incorrect for serial positions five and six. This measure allows us to determine where in a given sequence subjects have particular difficulty producing items, thus providing a measure of both item and order information (Fig. 1).

Statistical analysis

Trials on which a subject failed to begin with an open hand were excluded from analysis because they were likely to have reflected a premature start of the imitation. Trials were also excluded if subjects produced more than ten static gestures, as such responses likely reflected a brief pause during a transition that resulted in incorrectly identifying a static gesture. A total of 96% of trials were included in the analysis. Each dependent variable was subjected to an ANOVA with repetition (1–10) and feedback (present or absent) as within-subject factors, and sex (male and female) as the between-subject variable. Partial eta-squared (η_p^2) was used as our measure of effect size. A significance threshold of 0.05 was used throughout, and Hunyh-Feldt corrections were applied where sphericity assumptions were violated. Wherever significant effects or interactions were observed for sequence repetition, a post hoc analysis using a t-test contrasted the first and the tenth repetition, as a measure of learning.

Results

Imitation of single static gestures

We analyzed subjects' performance when they were required to imitate single static gestures. After the algorithm had segmented the subjects' movements for each of the static movements, it determined whether the imitation contained the correct gesture. Out of the 16 static gestures, both males and females correctly imitated the same number of gestures (females: mean = 11.44, SEM = 0.56; males: mean = 11.44, SEM = 1.25).

Imitation of sequences of gestures

Spatial errors With additional opportunities to view and imitate a sequence, subjects produce more gestures. The number of gestures produced reflects two kinds of influences: omissions and intrusions. Subjects produce fewer omissions (Fig. 3a) with learning ($F_{(2.847,45.557)} = 25.946$, $P < 0.001$, $\eta_p^2 = 0.619$). Post hoc analysis, comparing the first to the tenth repetition, confirms this finding ($t = 6.564$, $df = 17$, $P < 0.001$). In addition, sex significantly influences the number of omissions that subjects make ($F_{(1,16)} = 5.435$, $P = 0.033$, $\eta_p^2 = 0.254$), with males omitting more gestures than females. This suggests a female advantage in motor planning (Fig. 1b). There was a significant interaction between feedback and repetition for omissions ($F_{(9,144)} = 2.885$, $P = 0.004$, $\eta_p^2 = 0.153$). However, post hoc analysis reveals a significant effect of learning for both feedback ($t = 5.649$, $df = 17$, $P < 0.001$) and no feedback ($t = 7.445$, $df = 17$, $P < 0.001$) conditions. For omissions, there was a non-significant main effect of feedback and non-significant interactions between feedback and sex, repetition and sex and feedback, repetition and sex. There was also a significant effect of learning for intrusions ($F_{(7.743,123.886)} = 3.358$, $P = 0.002$, $\eta_p^2 = 0.173$), with subjects producing fewer intrusions for the first (mean = 0.014) compared to the last (mean = 0.194) repetition ($t = -2.6$, $df = 17$, $P = 0.019$). For intrusions, there were non-significant main effects of feedback and sex and non-significant interactions between feedback and sex, repetition and sex, feedback and repetition, and feedback, repetition and sex.

The accuracy of reproducing gestures was also examined. We observed a significant effect of learning for Gesture-Level errors ($F_{(9,144)} = 3.705$, $P < 0.001$, $\eta_p^2 = 0.188$). However, a significant interaction between repetition and sex ($F_{(9,144)} = 2.176$, $P = 0.027$, $\eta_p^2 = 0.120$) was also observed (Fig. 3b). Post hoc analysis revealed that the main effect of learning is driven by a significant reduction in Gesture-Level errors as a function of learning for females ($t = 3.601$, $df = 8$,
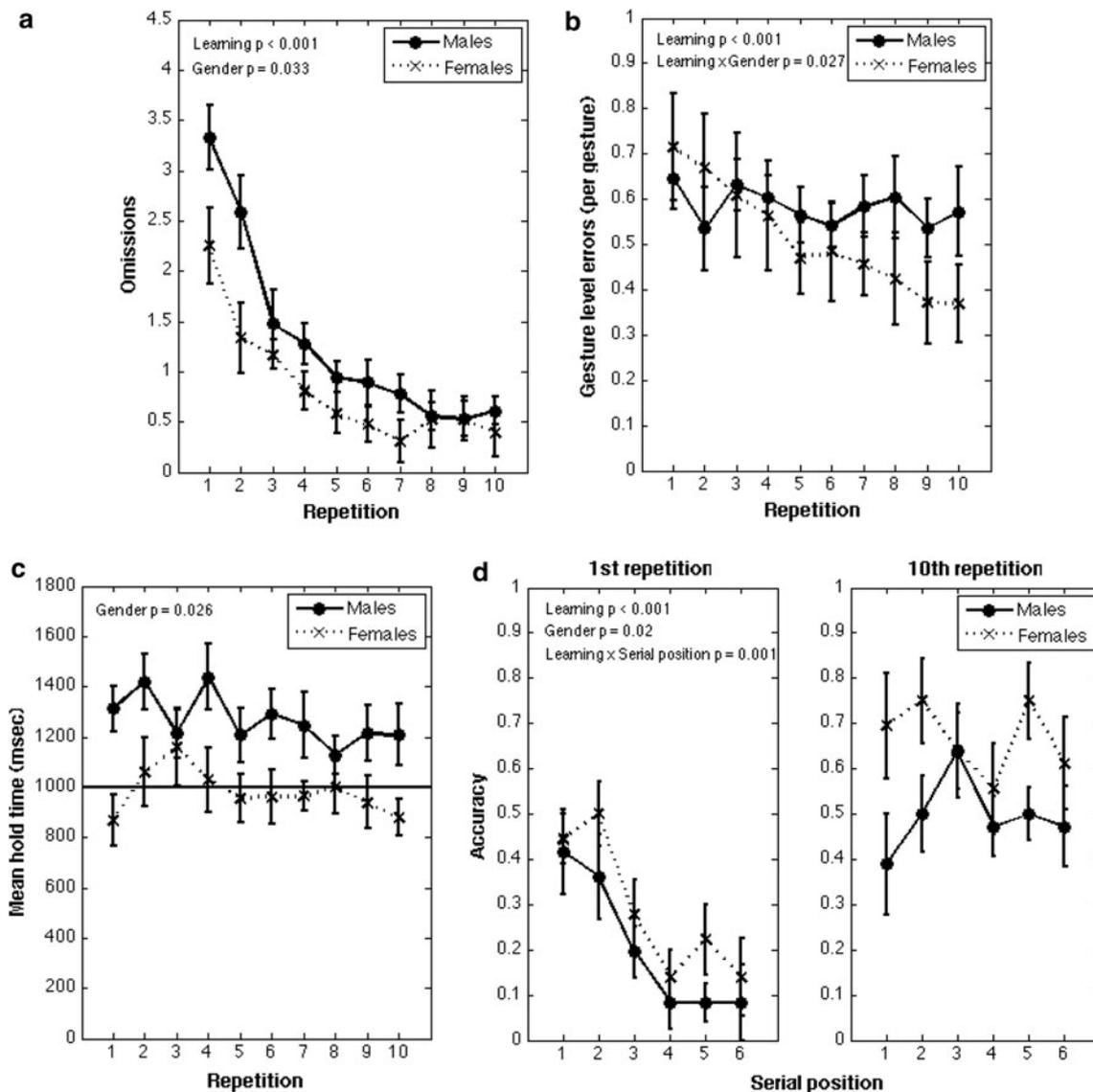
Fig. 3 a Mean number of omissions in a reproduced sequence as a function of a sequence's repetition. *Error bars* represent between-subject standard errors. Fewer omissions are produced as subjects learn the sequences and females produce fewer omissions than males, reflecting a female advantage in motor planning. **b** Mean number of Gesture-Level errors per gesture as a function of model sequence repetition. *Error bars* represent between-subject standard errors. With repetition, only females produce fewer Gesture-Level errors, reflecting a female advantage in the acquisition of the sequences. **c** Mean hold time as a function of the repetition of a model sequence. *Error*

bars show between-subjects standard error. This illustrates that males tend to hold each static gestures longer than females did, reflecting a female advantage at movement planning; this is highlighted by the fact that the average hold time of the model was 1,000 ms, which corresponds to the horizontal line at $y = 1,000$. **d** Serial position curves for the first (*left panel*) and last (*right panel*) repetition of a gesture sequence. Note that a higher value on the *y*-axis represents increased accuracy. This data illustrates a large primacy effect for the first repetition, which disappears by the tenth repetition as subjects learn the latter gestures within the sequence

$P = 0.007$) but not for males ($t = 0.754$, $df = 8$, $P = 0.472$); this suggests a female advantage in skill acquisition at the motor planning stages (Fig. 1b). For Gesture-Level errors, there were non-significant main effects of feedback and sex and non-significant interactions between feedback and sex, feedback and repetition, and feedback, repetition and sex. Repetition of a sequence produced a significant reduction in the number

of Sequence-Level errors ($F_{(6.123, 97.965)} = 4.262$, $P = 0.001$, $\eta_p^2 = 0.210$); this finding was confirmed by post hoc analysis ($t = 3.378$, $df = 17$, $P = 0.004$) with subjects producing more Sequence-Level errors on the first (mean $= 0.282$) compared to the last (mean $= 0.082$) repetition. For Sequence-Level errors, there were non-significant main effects of feedback and sex and non-significant interactions between feedback and sex,

repetition and sex, feedback and repetition, and feedback, repetition and sex.

Temporal components Sex significantly affected the mean hold time ($F_{(1,16)} = 5.993$, $P = 0.026$, $\eta_{\mathrm{p}}^2 = 0.272$), with males holding a gesture about 30% longer than females did (Fig. 3c). For hold time, there were non-significant main effects of feedback and repetition and non-significant interactions between feedback and sex, repetition and sex, feedback and repetition, and feedback, repetition and sex. In addition, the mean transition time was significantly affected by the availability of feedback during the reproduction of what had been seen ($F_{(1,16)} = 5.909$, $P = 0.027$, $\eta_{\mathrm{p}}^2 = 0.270$). In particular, transition times were longer when feedback was available (mean = 726.57 ms) than when no feedback was available (mean = 648.34 ms). This effect of feedback may reflect the fact that when subjects are able to see a display of their own movements, they exploit this visual feedback in order to fine-tune their movements in real time. For transition times, there were non-significant main effects of sex and repetition and non-significant interactions between feedback and sex, repetition and sex, feedback and repetition, and feedback, repetition and sex.

Serial position An analysis of the serial position curves (Fig. 3d) showed main effects of repetition ($F_{(1,16)} = 59.730$, $P < 0.001$, $\eta_{\mathrm{p}}^2 = 0.789$) and of a gesture's serial position ($F_{(5,80)} = 4.906$, $P = 0.001$, $\eta_{\mathrm{p}}^2 = 0.235$). Furthermore, there was a significant interaction between repetition and serial position ($F_{(5,80)} = 4.011$, $P = 0.003$, $\eta_{\mathrm{p}}^2 = 0.200$). This is due to a large primacy effect (i.e., increased accuracy for items that appear early in the sequence) for the first repetition (Fig. 3d, left). However, by the tenth repetition, the primacy effect has disappeared (reflected by a flattening of the serial position curve) as subjects learn the later segments within the sequence (Fig. 3d, right). Sex's significant main effect on the serial position curves ($F_{(1,16)} = 6.648$, $P = 0.02$, $\eta_{\mathrm{p}}^2 = 0.294$) shows that the female advantage on the imitation of these sequences is independent of how familiar the sequence is (that is how many times the sequence has been repeated) and holds over the entire sequence (that is the shape of the curve is not altered by subjects' sex). For the serial position analysis, there was a non-significant effect of feedback and non-significant interactions between feedback and sex, repetition and sex, serial position and sex, feedback and repetition, feedback, repetition and sex, feedback and serial position, feedback, serial position and sex, repetition, serial position and sex, feedback, repetition and serial position, and feedback, repetition, serial position and sex.

Experiment 2

Experiment One demonstrated several sex differences in the reproduction of motion sequences. Experiment Two sought to verify that these differences arise at the reproduction stage rather than at the encoding stage. This experiment used a different task in which male and female subjects watched two successively presented motion sequences, a "model" sequence and an "imitation" sequence. The imitation sequence represented an attempt at imitating the preceding model sequence. One or more errors were introduced into some of the imitation sequences. Both sequences were computer generated and of the same type as the stimuli used in Experiment One. The subjects' task was to rate the fidelity of the imitation shown to them, without imitating any of the sequences themselves.

Method

Subjects

Twenty-two subjects were recruited according to the same criteria as outlined for Experiment One. There were 11 males (mean = 22.64 years old, SD = 6.2) and 11 females (mean = 22.45 years old, SD = 3.62).

Stimuli

Two types of stimuli were generated: model sequences and imitation sequences. Seven model sequences were generated in the same way as outlined for Experiment One, and each comprised six different gestures. Fourteen imitation sequences were also generated. Two of these imitation sequences were a perfect match to two of the model sequences. For the remaining twelve imitation sequences, one or another kind of error was intentionally introduced with respect to the model sequences. These errors caused the computer-generated imitation to deviate in some predefined way from its model. Our intention was to assess how various error types affected subjects' judgments of an imitation's fidelity to its model. The different types of imitation sequences are outlined in Table 1. Note that the temporal dynamics of the model and imitation sequences were identical to those described for Experiment One.

Procedure

Subjects were instructed that they would view a model sequence comprising six different gestures. When the model sequence was completed, it was followed 1 s later by the computer-generated imitation sequence. The words "MODEL" and "IMITATION" were displayed at the top

Table 1 The different types of imitation sequences generated for Experiment 2

Imitation sequence type	Description
Type 1	A perfect reproduction, where no errors occurred
Type 2	One Gesture-Level adjacency error, where one gesture was produced incorrectly due to the swapping of two adjacent digits
Type 3	One Gesture-Level non-adjacency error, where one gesture was produced incorrectly due to the swapping of two non-adjacent digits
Type 4	One Omission, where one gesture was omitted from the imitation
Type 5	Two Gesture-Level adjacency errors, where two gestures were produced incorrectly due to the swapping of adjacent digits
Type 6	One Sequence-Level adjacency error, where two adjacent gestures were transposed
Type 7	One Sequence-Level non-adjacency error, where two non-adjacent gestures were transposed

of the screen during presentation of the corresponding stimulus. Once both the model and imitation had been viewed, subjects were prompted to rate the fidelity of the imitation on a scale of 0–100, where 100 was a perfect imitation and 0 was a totally incorrect imitation. Subjects viewed each of the 14 model-imitation pairs twice, in a randomized order.

Analysis

In order to determine the severity of each error type as rated by the subjects, we computed the difference between the ratings for perfect imitations (Imitation Type 1) and the given error type (Imitation Types 2–7) for each subject. These data were subjected to an ANOVA with error type (Types 2–7) as within-subjects factors and sex (male and female) as the between-subject variable. Partial eta-squared (η_p^2) was used as our measure of effect size. A significance threshold of 0.05 was used throughout, and Hunyh-Feldt corrections were applied where sphericity assumptions were violated.

Results

The mean severity rating score for each error type is illustrated in Table 2. There was a significant effect of error type ($F_{(5,100)} = 8.036$, $P < 0.001$, $\eta_p^2 = 0.287$); however, there was a non-significant effect of sex and a non-significant interaction between error type and sex.

Discussion

Experiment One required subjects to view a sequence of gestures, and then reproduce this sequence, while paying attention to item information (i.e., what each component gesture in a sequence was) and also order information (i.e., the order that items occupy in a sequence). Performance on

Table 2 Mean severity rating for each error type

Error type	Males	Females
1 Gesture-Level adjacency error	0.08 (0.30)	0.16 (0.09)
1 Gesture-Level non-adjacency error	0.16 (0.16)	0.20 (0.13)
1 Omission	−0.06 (0.31)	0.07 (0.11)
2 Gesture-Level adjacency errors	0.31 (0.20)	0.27 (0.18)
1 Sequence-Level adjacency error	0.06 (0.22)	0.16 (0.16)
1 Sequence-Level non-adjacency error	0.11 (0.35)	0.22 (0.14)

Standard deviations are shown in parentheses

this task involves a series of computations, in Fig. 1 we offer a proposal for what these computations might be. Our analysis of subjects' performance exploited a battery of dependent measures, each presumably reflecting a distinct computation. Overall, our results confirm the female advantage observed previously in the reproduction of hand movements (Chipman and Hampson 2006) and extend this finding to the acquisition of novel movement sequences. In addition, the detailed spatio-temporal analysis afforded by our paradigm and analytical algorithm allows us to isolate the components of gesture production where females are more efficient.

Our results show that males omit more gestures from their reproductions than females do (Fig. 3a). We believe that this difference reflects a female advantage at the level of individual items, that is, when it comes to motor planning. In addition to this generalized female advantage, females develop a further advantage over male participants as the sequences are learned. In particular, despite the fact that males produce more gestures as they view the sequences, they show no learning curve for Gesture-Level errors (Fig. 3b); this shows that the additional segments they are attempting to imitate are produced with errors. Contrariwise, with successive repetitions of a sequence, females produce more gestures and produce these with increased accuracy (Fig. 3b). The results with both

omissions and Gesture-Level errors demonstrate a female advantage at the level of motor planning.

An analysis of the temporal data showed that males hold each gesture about 30% longer than females do (Fig. 3c). In a model sequence, each gesture was held for 1,000 ms, a value that was very close to female subjects' mean hold time. The male subjects, on the other hand, held each gesture for ∼1,300 ms, suggesting that they hesitated more than females did before initiating the next component in a sequence. We posit that this hesitation reflects difficulty with movement planning, in other words generation of the motor command to move from one component gesture to another. One other potential explanation for this finding is that the males overestimated the time that the model held each of the gestures. We do not believe that this can account for this finding as we observed no effect of sex on transition times, and it seems unlikely that males would overestimate hold times but not transition times.

It is also important to consider the components of the task on which female subjects did not show an advantage. An analysis of the Sequence-Level errors shows no sex-related difference, suggesting that the female advantage is specifically associated with the reproduction of item information and not with order information. We also found no influence of sex on the number of intrusions into a reproduced sequence. This suggests that the general advantage that females enjoyed in our task cannot be accounted for by some advantage in monitoring and correcting the movement. Finally, we showed that females and males did not differ in their time taken to transition from gesture to gesture, which reflects movement execution. Overall, the dependent variables unaffected by sex suggest that the female advantage does not lie at the level of movement execution, online control, or ordering.

The serial position results (Fig. 3d) also provide important insights into the sex differences in this task. Although the heights of the serial position curves show a general female advantage with item information, the shapes of those curves show no systematic difference between sexes. This demonstrates that females' general advantage in performance does not come from more accurate information about sequence order. The shapes of these curves may also be informative for understanding how subjects are learning the gestures, as they indicate that subjects first learn gestures that appear early in the sequence, and then build on this information as they learn gestures later in the sequence during later repetitions. Importantly, both males and females appear to use this strategy to learn the sequence.

We also examined visual feedback's influence on performance. In doing this, we were especially interested in how feedback might differentially influence acquisition of this task by males and females. A previous study with a

different praxis task showed that males seem to rely more heavily on visual feedback than females do (Chipman et al. 2002). However, our results showed no such sex difference in the effect of visual feedback on behavioral performance. Our results did show that subjects took longer to transition between component gestures when visual feedback was available, presumably because they used the visual feedback to fine-tune the execution of their movements. Consistent with our behavioral data, an equal number of males and females reported that they found the feedback helpful. It should be noted that the visual feedback in our study comprised a real-time computer-generated animation of the subjects' movements, not the actual hand movements themselves. We chose this form of feedback because studies have shown the usefulness of virtual reality paradigms in stroke rehabilitation (Adamovich et al. 2009). As a result, we were interested in assessing how this virtual-reality form of visual feedback might be influenced by sex. In addition, when learning a skill by imitation, the feedback we receive is normally congruent with the stimulus we are imitating and so we wanted our feedback to conform to this general rule. We acknowledge that the type of feedback used in our study might, however, limit the generalizability of this particular finding related to visual feedback.

Experiment One assessed sex differences in gesture production. However, it was possible that any differences observed could be accounted for by differences originating from the stimulus presentation stage, where the sequence is initially encoded. The encoding of the sequence calls upon multiple cognitive processes including perception, attention and working memory. Therefore, our results could reflect female subjects' advantage in one or more cognitive processes for which sex differences have been already demonstrated (for review, see Halpern 2000). To rule out such an explanation, Experiment Two compared males and females on their ability to rate the fidelity of imitated sequences. This task requires the same initial encoding processes as Experiment One but does not require the reproduction of any movement sequence. Males and females performed comparably on this rating task, suggesting that the sex differences observed in Experiment One did not arise from some sex difference in failures at the level of stimulus encoding.

Our findings are consistent with reports of an anatomical difference in the organization of the system that supports the behavior tested in our study. In particular, Kimura (1983) has shown that apraxia is more often seen in females following left hemisphere lesions anterior to the central sulcus, whereas there is no anterior/posterior distinction for male apraxia patients. Our findings, taken together with Kimura (1983), suggest that the male disadvantage on praxis tasks arises from errors in motor planning, which depends upon anterior neural regions such

as the supplementary motor area (SMA) and dorsolateral prefrontal cortex (Hanakawa et al. 2008). This position is also supported by findings that indicate a role of the left premotor cortex in movement selection (see Rushworth et al. 2003, for a review), a critical part of motor planning. Our results also support some recent research demonstrating sex differences in the human mirror neuron system (Cheng et al. 2008).

To conclude, our results support the demonstration of Chipman and Hampson (2006) of a female advantage in the reproduction of gesture sequences, and support the idea that this female advantage operates at the level of motor planning, and cannot be accounted for by a sex advantage on processes such as motor execution or online control. Further, our results show that this female advantage is specific to producing the items within a sequence but not for ordering sequential items. In addition, we show that the female advantage extends to novel movement sequences and to the acquisition of such sequences. This claim about the breadth of the female advantage is consistent with the demonstration of a female advantage on gesture imitation for non-representational gestures as well as everyday gestures in preschoolers (Chipman and Hampson 2007). Our findings, along with this prior research, suggest that teaching strategies should take account of this sex difference. Moreover, future research might focus on ways in which the male disadvantage that we observed in motor planning could be compensated for. Finally, our data suggest that male and female apraxia patients may benefit from different rehabilitation techniques, and future research should attempt to isolate the best sex-sensitive strategies for rehabilitation.

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