

# Nonvisual Motor Training Influences Biological Motion Perception

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## Summary

Experimental evidence suggests a link between perception and the execution of actions [1–12]. In particular, it has been proposed that motor programs might directly influence visual action perception [13]. According to this hypothesis, the acquisition of novel motor behaviors should improve their visual recognition, even in the absence of visual learning. We tested this prediction by using a new experimental paradigm that dissociates visual and motor learning during the acquisition of novel motor patterns. The visual recognition of gait patterns from point-light stimuli was assessed before and after nonvisual motor training. During this training, subjects were blindfolded and learned a novel coordinated upper-body movement based only on verbal and haptic feedback. The learned movement matched one of the visual test patterns. Despite the absence of visual stimulation during training, we observed a selective improvement of the visual recognition performance for the learned movement. Furthermore, visual recognition performance after training correlated strongly with the accuracy of the execution of the learned motor pattern. These results prove, for the first time, that motor learning has a direct and highly selective influence on visual action recognition that is not mediated by visual learning.

## Results and Discussion

Our experiment consisted of three phases: a visual pretest, a nonvisual motor training procedure, and a visual posttest. The visual test was based on the discrimination of point-light walkers. These stimuli consist of a small number of dots that move like the joints of a human actor. Such stimuli induce a vivid percept of a moving person [14]. It has been shown that the human visual system processes them with high sensitivity and can extract fine details about actions from them [15–18]. Normal human gait patterns are characterized by a phase difference of approximately 180° between the two opposite arms and between the two opposite legs. We manipulated this phase difference in order to create three prototypical point-light walkers, corresponding to phase differences of 180°, 225°, and 270° (Figure 1). On each trial of the

visual test, participants were consecutively presented with two point-light stimuli. One of the stimuli was always one of the prototypes. The other stimulus was either the same prototype (in 50% of the trials) or a point-light walker with a slightly higher or lower phase difference than the prototype. In a forced-choice paradigm, participants had to report whether they perceived the two presented gait patterns as identical.

The second phase of our experiment consisted of the nonvisual motor training. Participants were trained to produce arm movements that matched the arm movements of the gait pattern with a phase difference of 270°. It has been shown that this coordination pattern typically cannot be executed spontaneously without prior motor training [19]. During motor training, participants were blindfolded, preventing them from any type of direct visual stimulation. Feedback was provided only verbally and haptically by the experimenter, carefully avoiding explicit rhythm cues (see [Experimental Procedures](#) for details). At the end of the motor training, the hand trajectories during execution of the learned motor pattern were recorded by a motion capture system. Recorded trajectories were used to evaluate the motor execution of the learned movement. The third phase of our experiment was a repetition of the visual test, in exactly the same way as before the motor training.

Figure 2 illustrates the visual recognition performance before (A) and after (B) training for the three prototypes (with phase differences of 180°, 225°, and 270°). Visual performances were evaluated by computing the percentages of “same” responses in trials in which the two stimuli had identical phase differences. The first important result of our study was that a substantial improvement in visual performance occurred only for the gait pattern that matched the trained arm movement (from 63% before motor training to 72% after training;  $p < .05$ , Tukey’s HSD). For the other two conditions (180° and 225°), results before and after training were not statistically different ( $p = .30$  and  $p = 1$ , respectively, Tukey’s HSD).

Since our experimental procedure prevented direct visual stimulation during training, the observed motor-visual transfer suggests a direct influence of the learned novel motor program on visual recognition that is independent of visual learning. Furthermore, this influence seems to be selective for the trained pattern, since the visual performance showed no increase for the untrained phase relationships (180° and 225°). This selectivity rules out unspecific learning effects, e.g., for the discrimination task or biological motion perception in general, as explanation for our data.

Even stronger evidence for a direct influence of motor programs on action recognition can be derived from an analysis of the covariation of visual recognition and motor performance after training. Indeed, if motor programs selectively influence visual recognition, then subjects who learned the novel motor pattern very well should also show a stronger improvement in the visual

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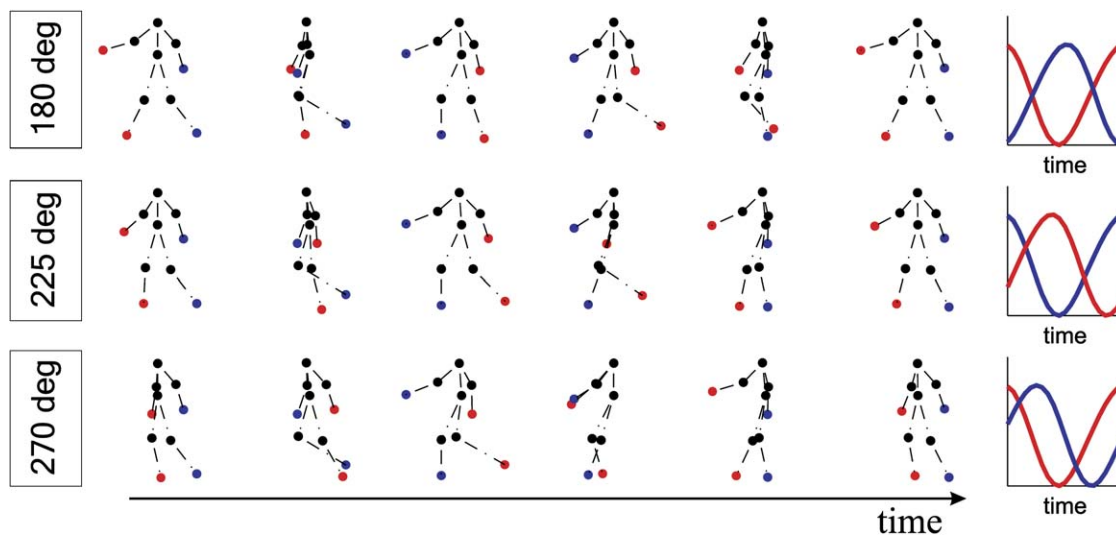


Figure 1. Stimuli for the Visual Discrimination Test

The top row shows successive frames of a point-light walker with a phase difference of 180° between the two arms and the two legs, corresponding to normal walking. The other two rows illustrate the prototype stimuli that were generated by manipulation of the phase difference between contralateral limbs (middle row, 225°; bottom row, 270°). Right panels show the horizontal components of the trajectories of the two hands. (The dots of the real stimuli had all the same color, and the underlying skeleton, indicated by the dashed lines, was not shown.)

recognition performance, but only for the trained pattern. To test this prediction, we correlated, over all subjects, the performances in the visual test with quantitative measures for the accuracy of the executed novel motor pattern after training. These accuracy measures were derived from the recorded hand trajectories.

We used two quantitative measures of motor performance (see [Experimental Procedures](#) for details). The first measure characterizes the smoothness of the executed movements. [Figure 3](#) shows the hand trajectories of two participants for normal walking, corresponding to a phase difference of 180° (A and B), and for the trained motor pattern corresponding to a phase difference close to 270° (C and D). Subject 1 could learn the novel motor pattern correctly, and produced smooth trajectories

close to purely sinusoidal motion for both gait patterns. Subject 2 learned the novel motor pattern rather poorly and produced smooth motion only for normal walking. For this subject, the hand trajectories for the trained novel pattern were jerky and deviated substantially from a purely sinusoidal motion. Based on a Fourier analysis of the hand trajectories, we defined a motor performance index,  $I_{sin}$ , that quantifies how closely the executed hand movement matches smooth purely sinusoidal motion (see [Supplemental Data](#), available with this article online, for details). The second index of motor performance,  $I_{stab}$ , was the variability of the relative phase of the hand movements (see [Supplemental Data](#) for details). This index is well established in the study of periodic bimanual coordination patterns. Well-learned

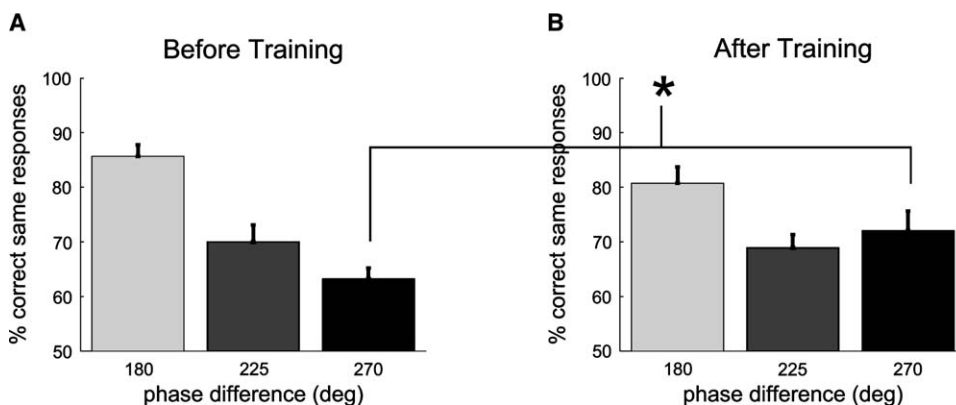


Figure 2. Visual Recognition Performance before and after Nonvisual Motor Training

The two panels show the percentages of “same” responses in trials in which the two stimuli had the same phase difference for the three prototypes (180°, 225°, and 270°). (A) shows performances before motor training, while (B) shows performance after motor training. Vertical bars indicate standard errors over eight participants. Visual recognition performance for the trained gait pattern showed a statistically significant increase after motor training ( $p < .05$ , Tukey’s HSD). The differences for the two untrained phase relationships were nonsignificant ( $p = .30$  and  $p = 1$  respectively; Tukey’s HSD).

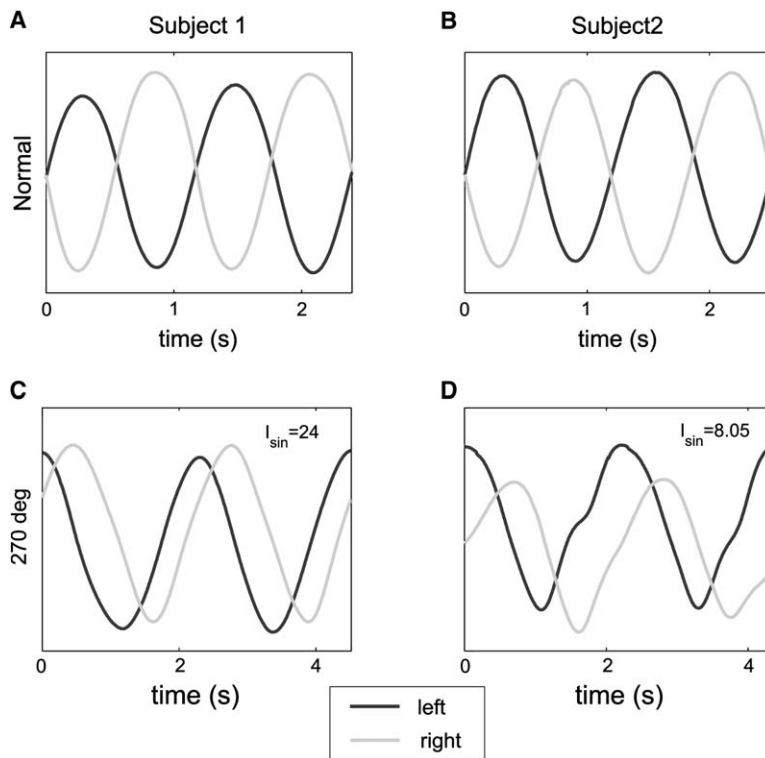


Figure 3. Hand Trajectories for Normal Walking and for the Acquired Novel Motor Pattern. Hand trajectories of two participants during normal walking with a phase difference of 180° (A and B) and for the trained novel pattern with a phase relationship of 270° (C and D). Subject 1 (left column) learned the novel motor pattern well, resulting in smooth trajectories for both patterns. Subject 2 (right column) learned the novel motor pattern rather poorly, resulting in smooth sinusoidal motion for the familiar pattern (180°) but nonsinusoidal movement for the novel pattern (270°). Numbers in the insets signify values of the index  $I_{sin}$  of motor learning for the two subjects (see Experimental Procedures for details).

patterns are characterized by a low variability of the relative phase [19].

Figure 4 shows scatter plots of the two motor performance indices  $I_{sin}$  and  $I_{stab}$  against the performance in the visual test for the stimulus with a phase difference of 270°. For both indices, motor and visual performance correlated significantly, but *only* after the motor training

(Spearman rank correlations:  $r_s = .91$ ,  $p < .005$  for the index  $I_{sin}$ ;  $r_s = -.90$ ,  $p < .005$  for the index  $I_{stab}$ ). Visual performance for the untrained gait patterns (180° and 225°) did not correlate significantly with the motor performance, neither before nor after the motor training. The same pattern of correlations was found when visual performance was measured using  $d'$  values in order

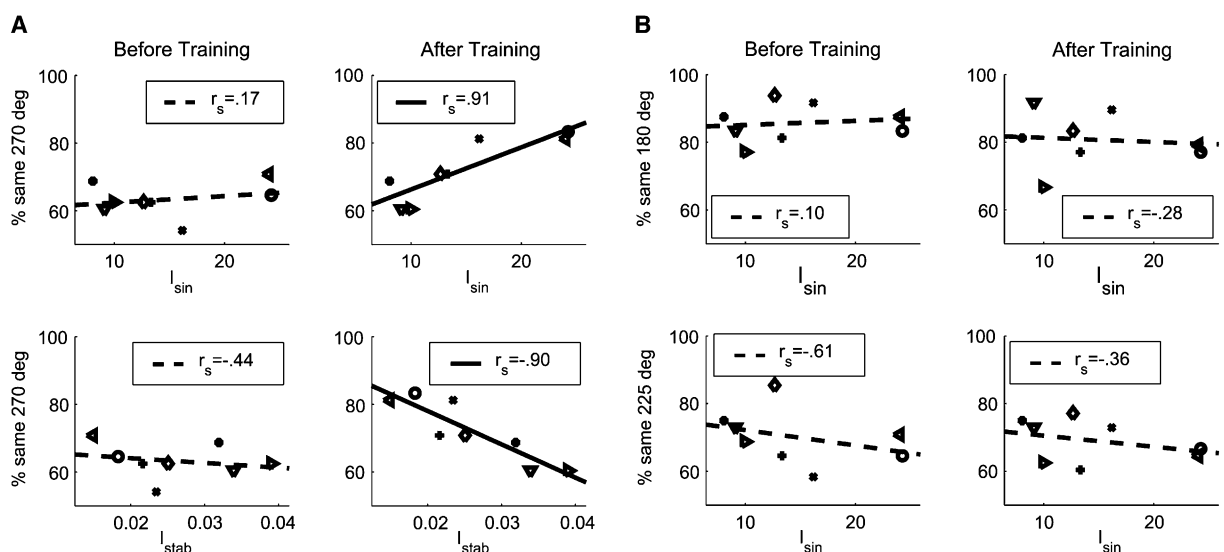


Figure 4. Scatter Plots of Visual Performance against Indices of Motor Performance

(A) Visual performance for the trained phase relationship 270° before and after training plotted against motor performance index  $I_{sin}$  (top) and motor performance index  $I_{stab}$  (bottom).

(B) Visual performance for the untrained phase relationships 180° and 225° plotted against the index of motor performance  $I_{sin}$  before and after training. Different symbols represent data from different subjects. Correlations for the index  $I_{stab}$  exhibited the same pattern of significances. In the two panels, significant correlations are indicated by solid regression lines ( $p < 0.005$ ). Numbers in the insets signify Spearman rank correlations.

to exclude response bias effects (see [Tables S1 and S2](#) for all significance values). Thus, in agreement with our prediction, after the motor training, participants who could execute the novel motor pattern with higher accuracy also exhibited increased sensitivity for its visual recognition.

One possible explanation of the observed motor-visual transfer is that the participants might have picked up the rhythm that characterizes the trained motor pattern, but not necessarily the details of the learned body movement. To rule out this possibility, we performed a control experiment in which the motor training was replaced by purely visual training. This training required subjects to discriminate stimuli that consisted of a pairs of squares that oscillated sinusoidally along the vertical axis. On each trial, subjects were presented with two successive stimuli at two different fixed positions on the screen. The first stimulus was a prototype with a phase relationship of 270°. The second stimulus was either identical to the first (50% of the trials), or its relative phase deviated from the first stimulus by an additional phase difference. Subjects had to judge whether the two stimuli were identical or not. Feedback was provided only every second session, whereas recognition performance was determined from the sessions without feedback. Participants were explicitly instructed to base their judgement on the “rhythm” of the observed oscillatory patterns. The visual tests before and after this training were identical to those in the first experiment. In spite of the instruction to attend to the rhythm, this modified training did not result in a significant improvement of performance for the trained phase relationship (270°) in the visual test (for details, see [Supplemental Data](#)). If the motor-visual transfer in our first experiment was predominantly based on the learning of a rhythm, a similar or even stronger transfer would be expected between the two visual tasks of this control experiment.

The visual recognition of actions is a central perceptual capability for humans and many other species. It has been hypothesized that motor programs might be involved in the recognition of actions [2, 3, 5–10]. However, under normal conditions (e.g., during the learning of novel movements in sports), motor and visual learning typically occur jointly at the same time. This makes it difficult to dissociate the influences of these two factors on visual action recognition. Our study shows, for the first time, a direct and highly selective influence of novel acquired motor programs on visual action recognition that is independent of visual learning. Moreover, our experiment demonstrates that motor learning, even when it is mediated exclusively by nonvisual sensory feedback, seems to influence visual action recognition in a very similar way as motor programs that have been acquired in the presence of visual feedback.

The observed influence of internal motor representations on biological motion recognition might be mediated by the visual imagination of motor patterns during the motor training. Indeed, experimental evidence suggests that motor imagination, action perception, and motor production might share common neuronal substrates [20–25]. Such imagination might be part of an “internal model” that supports the visual recognition of biological motion [26]. Also, our motor training might induce the learning of patterns of somatosensory activation that

are covertly activated during visual recognition, e.g., to support action understanding [27]. However, recent imaging studies have shown that the visual perception of point-light stimuli elicits activity in premotor cortex, but typically not somatosensory areas [28]. This suggests that motor programs might be the dominating factor that causes the observed motor-visual transfer.

Our experimental results show also that the link between the learned motor representation and visual action recognition is highly selective. After motor training, motor and visual recognition performance correlate on a subject-by-subject basis. Moreover, the training did not improve the recognition of movements that were only qualitatively similar to the learned pattern, e.g., with phase relationships 180° and 225°. This lack of visual generalization is compatible with a lack of motor generalization between these phase relationships [29]. In motor learning studies, it has been shown that the learning of bimanual tapping patterns with a phase relationship of 270° generalizes to the symmetric phase relationship of 90°, but not to other relative phases [19]. In addition to the observed highly selective link between motor programs and visual recognition, it seems possible that there exist also more unspecific influences that are not selective for a particular movement. For example, visually perceived motion might appear uniform if it has smoothness properties similar to those of human movements [4].

In addition, the fact that correlations between motor and visual performance increase after training suggests that the influence of motor representations on visual recognition builds up in parallel with the motor performance. Such parallel development seems consistent with observations in imaging experiments suggesting that during the acquisition of novel motor patterns, the focus of the neural activity shifts from prefrontal toward premotor and parietal areas [30]. Premotor and parietal areas have also been discussed as possible neural substrate of the interaction between action production and perception [5, 13].

Summarizing, our experiment demonstrates a direct and highly selective influence of motor representations on visual action perception, even if they have been acquired in the absence of visual learning. Future electrophysiological and imaging experiments as well as studies with neurological patients might help to unravel the neural structures that form the basis of this selective influence.

## Experimental Procedures

### Stimuli

To create novel unfamiliar motion patterns, we manipulated the relative timing of the opposite limbs of a point-light walker. While maintaining synchrony between pairs of contralateral limbs, we changed the phase differences between the opposite legs and opposite arms. We created three prototype patterns with phase differences of 180° (corresponding to normal walking), and 225° and 270° (representing unfamiliar gait patterns). From each of these three prototypes, six additional stimuli were created by adding further phase differences, ranging from –45° to 45° in steps of 15°.

### Visual Test

The visual recognition experiment was based on a forced-choice paradigm. In each trial, two point-light stimuli consisting of a total of nine dots were presented successively, at two different positions

on the screen. Each of these stimuli subtended an area of about  $8^\circ \times 5^\circ$ . The dots of the point-light stimuli had a diameter of  $0.3^\circ$ . In order to prevent participants from using low-level cues, the dots were jittered along the bones of the underlying skeleton (a stimulus manipulation similar to [31]). The life-time of the dots was 1 frame. Stimuli were presented on a Sony G520 monitor at a resolution of  $1024 \times 768$  pixels and a refresh rate of 120 Hz. Participants had to respond whether both stimuli represented the same gait pattern. Four cycles of each gait pattern were presented, each cycle lasting for about 1.2 s. The start position within the gait cycle was randomized across trials.

Experimental trials were organized into four blocks, each consisting of 72 trials. In half of the trials (12 per prototype), the two presented stimuli were identical. In the remaining trials, all possible combinations of each prototype with the six additional stimuli were presented with equal frequencies. The order of trials was randomized across blocks and participants. Only participants whose recognition performance were above chance level on the  $180^\circ$  condition and who exhibited a difference of at least 10% between recognition rates for the  $180^\circ$  and  $270^\circ$  conditions were included in the study and underwent the motor training. A total of nine participants were included. Data for one participant had to be discarded because she performed at chance level on all conditions after motor training.

### Motor Training

Participants were trained to execute an unfamiliar movement pattern with their arms. This movement corresponded to the arm movement of the gait pattern with a phase difference of  $270^\circ$ . The gait patterns with the unnatural phase relationships  $225^\circ$  and  $270^\circ$  would likely violate mechanical stability constraints for walking patterns, so that they cannot be executed, e.g., on a treadmill, without falling. However, experimental results have shown that coordination patterns can transfer spontaneously from arms to legs [32]. We thus trained only the coordination pattern for the arms. Our results show that the learned pattern transferred to the visual recognition of full-body movements.

Training was divided into sessions, each lasting for about 1 hr. Participants were blindfolded in order to prevent them from any visual stimulation. A special training procedure was applied that avoided explicit rhythm cues: participants were first instructed to learn four consecutive key postures in which the two hands were placed at well-defined positions relative to the body. Subsequently, the participants learned to move smoothly from one key posture to the next. During this training, only verbal and haptic feedback was provided about the appropriateness of the adopted postures and smoothness of the movements. Motor training lasted typically 3–4 sessions. It was terminated either when the participants were able to produce the novel motor pattern smoothly or if they exhibited no improvement during two consecutive sessions. Subjects executed the novel motor pattern at their most comfortable speed. They were never forced or instructed to move at a predefined speed similar to that of the visual stimuli. Subjects executed the novel motor patterns with cycle times in the range between 2.2 and 3.4 s, whereas the visual stimulus had a cycle time of about 1.2 s (typical for normal walking). This difference suggests that the observed motor-visual transfer does not critically depend on the speed of the performed gait pattern.

### Motion Capturing

After the motor training, the movements of the participants were recorded with a Vicon 612 motion capture system (Vicon Motion Systems Ltd, Oxford, UK) with seven cameras. The temporal sampling rate was 120 Hz, and the spatial error was less than 1 mm. Data was preprocessed with commercial software by Vicon and the trajectories were smoothed by a boxcar filter with a temporal window size of 0.1 s in order to eliminate high-frequency noise. Finally, the horizontal components of the sagittal projections of the trajectories of the left and right hand,  $x_L(t)$  and  $x_R(t)$ , were computed. Participants remained blindfolded also during the motion capturing.

### Computation of the Index $I_{sin}$ of Motor Learning

The trained motor pattern was a periodic pendular motion. For correct execution, the trajectories of the two hands should thus closely approximate a purely sinusoidal motion (Figure 3). The similarity of

the executed movement with purely sinusoidal motion can be derived from the Fourier transform of the hand trajectories, by dividing the power of the first harmonic by the power of the higher harmonics:

$$I_{sin} = \frac{|X_L(1)|}{\sqrt{\sum_{n=2}^N |X_L(n)|^2}} + \frac{|X_R(1)|}{\sqrt{\sum_{n=2}^N |X_R(n)|^2}}$$

$X_L(k)$  and  $X_R(k)$  represent the Discrete Fourier Transforms of the averaged hand trajectories. High values of this index indicate that the movement of the hands is close to a pure sinusoidal oscillation.

Hand trajectories were averaged over successive movement cycles. For the segmentation of the movement cycles, we computed the quantity  $\phi(t) = \arctan\left(\frac{\dot{x}_L(t)}{\dot{x}_R(t)}\right)$ . At the beginning of each gait cycle,  $\phi$  has the value  $-\pi$  and gradually increases until it reaches the value  $\pi$  at the end of the cycle. Hand trajectories were segmented into cycles by finding the discontinuity points of  $\phi(t)$ . After segmentation, each cycle was uniformly sampled with 500 discrete time steps. Average hand trajectories were defined as the means over these time-normalized segments.

### Computation of the Index $I_{stab}$ of Motor Learning

For coordinated periodic bimanual movements, the variability of the relative phase of the two hands has been shown to characterize the dynamic stability and the degree of consolidation of learned motor patterns [19]. To estimate the relative phase, we determined the time points of zero crossings of the trajectories  $x_L(t) - \bar{x}_L$  and  $x_R(t) - \bar{x}_R$  and their first derivatives  $\dot{x}_L(t)$  and  $\dot{x}_R(t)$ , where  $\bar{x}_L$  and  $\bar{x}_R$  represent the mean positions across time for the left and the right hands, respectively. These time points of the zero crossings and extrema of the trajectories of the right and left hand define two time series  $\psi_L(k)$  and  $\psi_R(k)$ . In the case of ideal performance, the right and the left hands move in exactly the same way, resulting in a constant difference between the two time series  $\psi_L(k) - \psi_R(k)$ . For sub-optimal performance, this difference fluctuates as a function of the index  $k$ . The quality measure  $I_{stab}$  was defined as the standard deviation of the difference  $\psi_L(k) - \psi_R(k)$  normalized by the average gait cycle time.

### Supplemental Data

Supplemental Data include two figures, three tables, and Supplemental Experimental Procedures and can be found with this article online at <http://www.current-biology.com/cgi/content/full/16/1/69/DC1/>.

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### References

- Ernst, M.O., Banks, M.S., and Bühlhoff, H.H. (2000). Touch can change visual slant perception. *Nat. Neurosci.* 3, 69–73.
- Prinz, W. (1997). Perception and action planning. *Eur. J. Cogn. Psychol.* 9, 129–154.
- Knoblich, G., and Flach, R. (2001). Predicting the effects of actions: interactions of perception and action. *Psychol. Sci.* 12, 467–472.



4. Viviani, P., and Stucchi, N. (1992). Biological movements look uniform: evidence of motor-perceptual interactions. *J. Exp. Psychol. Hum. Percept. Perform.* *18*, 603–623.
5. Rizzolatti, G., Fogassi, G., and Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat. Rev. Neurosci.* *2*, 661–670.
6. Shiffrar, M., and Freyd, J.J. (1990). Apparent motion of the human body. *Psychol. Sci.* *1*, 257–264.
7. Wilson, M., and Knoblich, G. (2005). The case for motor involvement in perceiving cospecifics. *Psychol. Bull.* *131*, 460–473.
8. Brass, M., Bekkering, H., Wohlschläger, A., and Prinz, W. (2000). Compatibility between observed and executed finger movements: comparing symbolic, spatial and imitative cues. *Brain Cogn.* *44*, 124–143.
9. Meltzoff, A.M. (1999). Origins of theory of mind, cognition and communication. *J. Commun. Disord.* *32*, 251–269.
10. Blakemore, S., and Frith, C. (2005). The role of motor contagion in the prediction of action. *Neuropsychologia* *43*, 260–267.
11. Hecht, H., Vogt, S., and Prinz, W. (2001). Motor learning enhances perceptual judgement: a case for action-perception transfer. *Psychol. Res.* *65*, 3–14.
12. Wohlschläger, A. (2000). Visual motion priming by invisible actions. *Vision Res.* *40*, 925–930.
13. Calvo-Merino, B., Glaser, D.E., Grezes, J., Passingham, R.E., and Haggard, P. (2005). Action observation and acquired motor skills: an fMRI study with expert dancers. *Cereb. Cortex* *15*, 1243–1249.
14. Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Percept. Psychophys.* *14*, 201–211.
15. Thornton, I.M., and Vuong, Q.C. (2004). Incidental processing of biological motion. *Curr. Biol.* *14*, 1084–1089.
16. Cutting, J.E., Moore, C., and Morrison, R. (1988). Masking the motion of human gait. *Percept. Psychophys.* *44*, 339–347.
17. Neri, P., Morrone, M., and Burr, D. (1998). Seeing biological motion. *Nature* *395*, 894–896.
18. Bertenthal, B.I., and Pinto, J. (1994). Global processing of biological motion. *Psychol. Sci.* *5*, 221–225.
19. Zanone, P.G., and Kelso, J.A.S. (1997). Coordination dynamics of learning and transfer: collective and component levels. *J. Exp. Psychol. Hum. Percept. Perform.* *23*, 1454–1480.
20. Jeannerod, M. (1997). *The Cognitive Neuroscience of Action* (Oxford, UK: Blackwell).
21. Jeannerod, M., and Decety, J. (1995). Mental motor imagery: a window into the representational stages of action. *Curr. Opin. Neurobiol.* *5*, 727–732.
22. Decety, J., Perani, D., Jeannerod, M., Bettinardi, V., Tadary, B., Woods, R., Mazziotta, J.C., and Fazio, F. (1994). Mapping motor representations with positron emission tomography. *Nature* *371*, 600–602.
23. Grossman, E., and Blake, R. (2001). Brain activity evoked by inverted and imagined biological motion. *Vision Res.* *41*, 1475–1482.
24. Rizzolatti, G., and Craighero, L. (2004). The mirror-neuron system. *Annu. Rev. Neurosci.* *27*, 169–192.
25. Stephan, K.M., Fink, G.R., Passingham, R.E., Silbersweig, D., Ceballos-Baumann, A.O., Frith, C.D., and Frackowiak, R.S.J. (1995). Functional anatomy of the mental representation of upper extremity movements in healthy subjects. *J. Neurophysiol.* *73*, 373–386.
26. Wolpert, D.M., Doya, K., and Kawato, M. (2003). A unifying computational framework for motor control and social interaction. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* *358*, 593–602.
27. Blakemore, S., and Decety, J. (2001). From the perception of action to the understanding of intention. *Nat. Rev. Neurosci.* *2*, 561–567.
28. Saygin, A.P., Wilson, S.W., Hagler, D.J., Bates, E., and Sereno, M.I. (2004). Point-light biological motion perception activates human premotor cortex. *J. Neurosci.* *24*, 6181–6188.
29. Poggio, T., and Bizzi, E. (2004). Generalization in vision and motor control. *Nature* *431*, 768–774.
30. Shadmehr, R., and Holcomb, H.H. (1997). Neural correlates of motor memory consolidation. *Science* *277*, 821–825.
31. Beintema, J.A., and Lappe, M. (2002). Perception of biological motion without local image motion. *Proc. Natl. Acad. Sci. USA* *99*, 5661–5663.
32. Kelso, J.A.S., and Zanone, P.G. (2002). Coordination dynamics of learning and transfer across different effector systems. *J. Exp. Psychol. Hum. Percept. Perform.* *28*, 776–797.