Perceptual Learning Immediately Yields New Stable Motor Coordination

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Keywords: Perception-action, rhythmic movement coordination, perceptual learning, movement stability

Abstract

Coordinated rhythmic movement is specifically structured in humans. Movement at 0° mean relative phase is maximally stable, 180° is less stable, and other coordinations can, but must be learned. Variations in perceptual ability play a key role in determining the observed stabilities, so we investigated whether stable movements can be acquired by improving perceptual ability. We assessed movement stability in Baseline, Post Training and Retention sessions by having participants use a joystick to coordinate the movement of two dots on a screen at three relative phases. Perceptual ability was also assessed using a 2-alternative forced choice task in which participants identified a target phase of 90° in a pair of displays. Participants then trained with progressively harder perceptual discriminations around 90°, with feedback. Improved perceptual discrimination of 90° led to improved performance in the movement task at 90° with no training in the movement task. The improvement persisted until Retention without further exposure to either task. A control group's movement stability did not improve. Movement stability is a function of perceptual ability, and information is an integral part of the organization of this dynamical system.

Rhythmic movement coordination is a paradigm case for the study of perception-action, because it involves all the essential features of a perception/action system (voluntary control of limb movements, coordination among multiple limbs or people, and online perceptual (informational) guidance and coupling of the voluntary movement). The key variable in studies of movement coordination is relative phase, a measure of the relative location of two oscillators within their cycles. 0° mean relative phase means that the two oscillators are at the same point in their cycle at the same time; 180° means they are at opposite ends of their cycle at the same time; and 90° is the point halfway in between these extremes.

Bimanual rhythmic movement coordination is very specifically structured in humans. 0° and 180° are the only two stable movement coordinations that people can spontaneously produce. Other coordinations can, but must, be learned (e.g. Wenderoth, Bock, & Krohn, 2002; Zanone & Kelso, 1992a, 1992b, 1997). Without training, movement at 90° is maximally unstable. Movement at 0° is more stable than at 180° and an increase in frequency leads to increased phase variability, more so at non-0° phase relations. There is (under a non-interference instruction) a spontaneous transition to 0° around 3-4Hz, with no tendency to transition from 0° to any other relative phase (Kelso, 1984; Kelso, Scholz & Schöner, 1986; Kelso, Schöner, Scholz & Haken, 1987).

This pattern is captured in the Haken-Kelso-Bunz model (HKB: Haken, Kelso & Bunz, 1985; see Kelso, 1995 for an excellent review) by a potential function. The function contains a steep well centred on 0° (representing that it is a very stable state), a less steep well centred on 180° (representing that it is stable, but less so) and no wells anywhere else (representing the lack of other stable states). However, this is an explicitly phenomenological model. The behavior simply arises in the model from the superposition of two cosine functions, with no reference to the system instantiating the behavior. In addition, Haken et al.'s talk of attractors (while a convenient descriptive shorthand) is not explanatory. They provided no account of the origin of the potential function. The question therefore remains – why is human rhythmic movement coordination patterned this way?

The Role of Perception: Movements that are trivial when performed in isolation become difficult to maintain when performed simultaneously as a coordinated movement (Rosenbaum, Dawson & Challis, 2006). This suggests that the constraint on task performance (a preference for symmetrical behaviour) emerges from the *coupling* entailed by coordination. There is strong evidence that the coupling is in general perceptual, or more precisely, *informational*. The movement phenomena persist when the oscillators belong to two different people (Schmidt, Carello & Turvey, 1990; Temprado, Swinnen, Carson, Tourment & Laurent, 2003) or when one of them is a simulated oscillator (Buekers, Bogaerts, Swinnen & Helsen, 2000; Wilson, Collins & Bingham, 2005a; Wimmers, Beek & van Wieringen, 1992). In these cases, the coupling was mediated completely by vision.

A series of perceptual studies had participants make judgments of phase variability in oscillators that were presented visually (Bingham, Schmidt & Zaal, 1999; Bingham, Zaal, Shull & Collins, 2000; Zaal, Bingham & Schmidt, 2000; Bingham 2004a, 2004b) and proprioceptively (Wilson, Bingham & Craig, 2003). Levels of phase variability are best discriminated at 0°. 180° is judged to be more variable than 0°, even with no added variability, and when there are added levels of variability, these are not as well discriminated. 90° is judged to be maximally variable (even in the absence of added variability) and the added levels of phase variability are not discriminated at all. As frequency was increased, 180° was judged to be increasingly variable and discrimination of phase variability got worse. In other words, discrimination of phase variability follows an inverted, asymmetric U-shaped function of mean relative phase, the same shape as the HKB potential function (see Zaal et al., 2000 for more detail).

The next step was to explicitly manipulate the perceptual information used to perform the task. Changing the information changes the stability of that movement. Bogaerts, Buekers, Zaal, & Swinnen (2003) transformed the visual feedback in a movement task (so that 180° movement produced 0° on a screen, or so that orthogonal movements produced parallel motion on a screen). They found that if the visual signal was at 0°, non-0° movements were stabilized, and orthogonal movements were stabilized by parallel feedback. Wilson et al.. (2005a) replicated this phenomenon using a different paradigm. Participants tracked a computer controlled moving dot on a screen with a joystick controlling a second dot. In one condition, participants moved so as to produce 0°, 90° or 180° between the two dots. Movement stability was an HKB shaped function of mean relative phase. In a second condition, the mapping between the joystick and the dot was altered, such that in order to produce 0° between the two dots, participants had to move at 90° or 180°. In these cases movement stability increased and did not show the HKB shape. These studies demonstrate that non-0° movements are not intrinsically unstable (see also experiments that manipulate the eigenfrequency of the oscillators involved, e.g. Schmidt & Turvey, 1994). If the participant can readily discriminate the information used to perform the task, then this stable perception allows for stable movement. Non-0° movements are unstable under normal conditions because the conditions do not allow the participant to clearly perceive the movement coordination. Our conclusion, therefore, is that movement stability is primarily a function of perceptual ability.

The evidence for the role of perception is compelling; however there are two other common places to look for a symmetry preference that should be noted. First, two separate attempts to model the phenomena have placed the coupling in the nervous system (Beek, Peper & Daffertshofer, 2002; Cattaert, Semjen & Summers 1999). Both of these approaches, however, fail to explain how the phenomena are preserved when the coupling is between people, or between a person and a computer display. While the nervous system is, of course, involved in these tasks, it cannot be that the HKB landscape is generated by confusion or interference between two separate neural systems driving limb movements. Second, Kelso's original (1984) paper specifically describes in-phase movement as entailing the coactivation of homologous muscle groups – simultaneous flexion and extension. Swinnen and colleagues (e.g. Swinnen, Jardin, Meulenbroek, Dounskaia, & Hofkens-Van Den Brandt, 1997) refer to this as the egocentric constraint (symmetry is defined with respect to the midline of the body). If making two functionally identical muscle groups act the same way at the same time is easier than making them act differently, the lower stability of non-0° phase relations would therefore reflect a bottleneck in our ability to activate coalitions of muscles. While it is empirically the case that such movements are more stable (Lee, Swinnen & Verschueren, 1995) the precise mechanism that leads to such a symmetry preference is not yet elaborated. Again, this fails to account for the phenomena persisting between people, and for the persistence of the phenomena when using non-homologous muscle groupings (e.g. coordinating a leg and an arm; Baldissera, Cavallari & Civaschi, 1982; Kelso & Jeka, 1992; Swinnen, Dounskaia, Verschueren, Serrien & Daelman, 1995). There is therefore a clear motivation to explore the nature of the perceptual coupling in these tasks.

Learning New Coordinations: It is possible to learn to move at phases other than 0° and 180°. In the first learning studies in this field (Zanone & Kelso, 1992a & b, 1997; Kelso & Zanone, 2002), participants were trained to move at 90° or 135° to investigate how this training generalized to other relative phases and effectors. Learning 90° was described by these authors as a qualitative change in the shape of the HKB potential function (a new attractor in the HKB potential function). Learning only generalized to the symmetry partner[1] of 90°, namely 270°. Participants who could already perform 90° were trained to perform 135°. In this case, instead, performance at 90° worsened as performance at 135° improved. The new skill again only generalized to the symmetry partner of 135° (225°). Kelso & Zanone (2002) found a similar pattern of results, but this time also showed that training a new coordination in one set of effectors (e.g. the arms) transferred to a different set of effectors (e.g. the legs). Kelso and Zanone interpreted their results as showing that what is learned is a high-level, abstract (but neurally implemented) dynamic representation of the action.

Another set of learning studies focused in more detail on how learning varies across different parameters that characterize performance (Wenderoth & Bock, 2001) or across different locations in HKB potential function space (Wenderoth et al.., 2002). Wenderoth & Bock showed that learning to perform 90° seemed to occur over three separable processes, each occurring on their own time scale. The fastest improvement was in average performance; next fastest was in precision; and slowest was improvements in switching time (the time taken to intentionally switch into 90° from another state). They equated these parameters with attractor location, attractor depth and the steepness of the attractor (Scholz & Kelso, 1990) respectively. This time scale ordering is sensible; you must first produce the target behaviour, and only then can your

[1] A symmetry partner is a coordination that is identical except for which oscillator is ahead and which is behind; in other words, movement stability is independent of which limb leads and which follows.

performance be constrained to a specific smaller region of the potential function space. This then allows for a period of consolidation in which variability is reduced, and the new pattern to become well learned (more stable).

Wenderoth et al.. (2002) trained participants to produce coordinations that were either 36°, 60° or 90° away from 0° or 180°. Participants were able to learn these coordinations but they were not learned in the same way, nor to the same extent. Zanone & Kelso (1994) had predicted that learning rate should vary inversely with the stability of the closest attractor, because competition between learning requirements and intrinsic coordination dynamics would become smaller with greater distance. Wenderoth et al.. actually found that patterns close to 0° were stabilized faster than patterns closer to 180° (replicating Fontaine, Lee & Swinnen, 1997). Wenderoth et al.. hypothesized that perception of the movements may be playing a key role, rather than competition between attractors. Specifically, they suggested that because visually presented phase relations close to 0° are more easily discriminated than those close to 180° (Zaal et al.., 2000), learning 36° is easier than learning 144° because the former can be easily discriminated from 0°, while the latter is not as easily discriminated from 180°. If a person cannot discriminate between two different movements, they will be unaware that they are moving incorrectly and hence be unable to improve. Learning follows perceptual discriminability.

Current Study: Learning studies all train people to move at a novel coordination by having them actually try to move at that coordination, paced by some external stimulus. But the characteristics of learning all suggest that it is not the movement, per se, that is being learned. First, learning a novel coordination allows you to move at the symmetry partner of that coordination for free; this suggests that the specific action being implemented during training (a particular limb leading or lagging) is not what is being acquired. Second, learning is not specific to the limbs instantiating the movement; for instance, learning to move at 90° generalizes from arms to legs (Kelso & Zanone, 2002). Kelso and Zanone discuss learning in terms of acquiring an abstract dynamical coordinative structure that defines how the limbs are to be controlled, but this, like the HKB model, is just a redescription of the phenomena. Third, learning a novel coordination follows the perceptual consequences of the coordination, and not the specific movements used to produce it (Atchy-Dalama, Peper, Zanone & Beek, 2005). So what is it that changes over the course of learning?

The judgment and movement studies clearly implicate a vital role for perception in determining movement stability (see also Mechsner, Kerzel, Knoblich & Prinz, 2001; Mechsner & Knoblich, 2004). The results of Bogaerts et al.. (2003) and Wilson et al.. (2005a), in which non-0° movements are stabilized by transformed feedback, suggest that movement stability is a function of perceptual ability: the reason 0° is easy while other relative phases are hard is that the requisite information is detected most readily at 0° and less so elsewhere. Improved stability of movement in the various learning studies therefore implies improved perceptual ability; what has changed, we suggest, is the participants' ability to detect the requisite information at the novel coordination.

The clear prediction, which the current study tests, is that if a participant were to improve his or her ability to detect the requisite information, their movement stability would improve. Specifically, the current experiment tested whether improving perceptual discrimination of the space around 90° led to improvements in movement stability at 90°. Participants were trained to be able to discriminate 90° from neighboring phases. We predicted that improved resolution would translate to an improved ability to maintain a movement at 90° in the absence of practice of the actual movement.

Methods

Participants: There were 12 participants (22-54 years old). All were right-handed, had normal or corrected-to-normal vision and were free from any known neurological defects or motor disabilities. Based on motor performance in the Baseline session, half the participants were assigned to the Experimental Group and half to the Control group (making the two groups matched on initial movement stability). Participants were paid $7 per hour for their time. Ethical approval was granted by the Institutional Review Board at Indiana University, Bloomington.

Design: There were two types of experimental task: 2-alternative forced choice (2AFC) *judgments*, and coordinated rhythmic *movement*. There were then two types of session:

1. *Assessment* (Baseline, Post Training) consisted of both judgment trials (at both 90° and 180°) and movement trials (moving at 0°, 90° and 180°). There was no feedback for any trial in the Assessment sessions. We also ran a third Assessment session (Retention) with just movement trials.
2. *Training* consisted only of judgement trials at 90° with feedback. There were no Movement trials during training.

The Experimental group did three assessment sessions and up to 14 training sessions (until improvement had plateaued – see below for criteria). All sessions were performed on different days. The final Training session and the first Post Training session were separated by at least one day, and Post Training and Retention sessions were separated by at least one week. The Control group did three sessions of movement trials only, with no training or feedback, timed similarly to the Experimental group's Assessment sessions.

Procedure

1. Judgments: Participants performed a series of 2AFC judgments on displays presented on a Power Mac G4. There were two tasks: 'Choose 90°' and 'Choose 180°'. Each trial consisted of a pair of successively presented stimuli (two dots (~15mm diameter) separated by ~35mm vertical distance moving harmonically on the screen at some mean relative phase, for 4s at 1Hz; the motion of both dots was centered at the screen centre, with amplitude of 300 pixels (~115mm). One of each pair showed two dots moving at the target relative phase (90° or 180°) and the other was either the same or different. 'Different' displays were the target +/- 9°, 18°, 27°, 36° and 45° and the target was either the first or second display – there were therefore 21 different trial types (10 different differences x 2 orders, plus a catch trial where both displays were the target). One demonstration trial of the target phase was given at the start of the Assessment session. No feedback was given during these trials in the Assessment sessions.

In each Training session participants performed 12 blocks of Choose 90° with feedback. The participants compared 90° to four other phases, two less than 90° and two greater then 90°. Over sessions the discrimination was made harder - differences 1 & 4 (initially 90° +/- 40°) were reduced by 10° between each set (to 90° +/- 30°, 20°, and 10°), and differences 2 & 3 (initially 90° +/- 20°) were reduced by 5° (to 90° +/- 15°, 10°, 5°). Each block had one repetition of each trial type, with the order of presentation randomized within block. Participants were told whether their response was correct or incorrect, and if incorrect were shown an example of 90°.

Performance in the Training set determined whether the participant progressed to the next hardest training set in the following session. If the participant was 85% correct for the largest discrimination level within a set then they progressed to the next training set for the next session, otherwise they repeated the current training set in the following session. The participant was, however, automatically moved to the next training set after four repetitions at the same level. Participants were trained for up to six sessions in the hardest discrimination set (refer to Table 1 for specific details). It is important to note that the training did not involve any additional practice at the movement task.

Data Analysis - Judgments: Data from this task were the frequency with which participants responded “90° First” or “180° First”. The data were analyzed with each trial being described by the magnitude of the phase difference. This places data from ’45-90’ trials and ‘135-90’ at the same point on the axis, specifically -45. The analogous sorting was also done for the Choose 180° data.

A nominal logistic regression model was fit separately to each data set. The absolute value of the mean relative phase difference at which the probability of responding ‘90° First’ was 25% and 75% was computed from each regression curve, and averaged. This provides a measure of the threshold (the magnitude of the difference required before participants were above chance in their discriminations).

2. Movement: Participants sat in front of a Power Mac G4, which was connected to a Logitech Force 3D Pro joystick (which had the force feedback feature disabled). The joystick sat on a keyboard tray so that participants could comfortably use the joystick but not see it. The computer presented a display of two dots, white on a black background, one above the other (screen refresh rate 60Hz, resolution 1024x768, for 30s). The top dot was under the control of the computer, and oscillated at 1.0Hz. The bottom dot was controlled by the participant using the joystick in a smooth, side to side movement (Figure 1 shows a schematic of this setup). The computer recorded the location of the joystick and computer controlled dots.

Participants were instructed to move so as to produce a mean relative phase of 0°, 180°, or 90°, 3 trials of each, blocked by phase and presented in the noted order. Each block began with a 4s demonstration of the required relative phase and a 30s practice trial (not analysed).

Data Analysis - Movement: A 60Hz position time series for both the computer- and person controlled dots was recorded. The full 30s of data were used, i.e. the time series was not trimmed at the start. After the experiment, these time series were filtered (using a low-pass Butterworth filter with a 10Hz cut-off frequency) and numerically differentiated to produce a velocity time series. The relative phase between the dots was computed at each time step as the difference between the arctangent of each dot's velocity divided by position with requisite corrections for the quadrants of the phase plane.

Relative phase is a circular variable, which creates a problem for calculating basic descriptive variables. There are numerous trigonometric methods for performing basic statistical tests (Batschelet, 1981; Fisher, 1993; Mardia, 1972; Jammalamadaka & SenGupta, 2001). The two most useful measures are the *mean vector* (θ), and the normalized length of this vector (*mean vector length*; MVL), which ranges from 0-1 and is a measure of within trial stability. We have used these variables previously (e.g. Wilson et al.., 2005a, 2005b). However, these tests assume that mean direction and stability are independent of one another, and one of the cardinal features of rhythmic movement coordination is that this is not true. MVL for a trial in which an untrained participant attempts 90° is often artificially elevated by them spending long periods of time stably producing, for instance, 0°; performance is indeed stable, but MVL is not reflecting their failure to maintain the target mean relative phase. Wilson et al.. (2005a) addressed this by regressing MVL against phase deviation, and using the intercept (when phase deviation = 0) as an estimate of the movement stability at the target phase.

Here, we have computed a new variable, *proportion time on task*, which solves the problem more efficiently. For each trial, we took the relative phase time series and computed the proportion of that time series that fell within the range of the target phase +/- a tolerance (here, set to 20°[2]). This measure ranges from 0-1 and effectively summarises stability of movement at the required relative phase in a single number.

Results

We first analysed the Judgment data to confirm that our Experimental participants had in fact learned as a result of their extensive training. Second, we analysed the Movement data to test the key question of this study – did the perceptual training lead to improved movement stability?

1. Judgments: We performed a repeated measures ANOVA on the mean threshold data from the Experimental group, with Phase (2 levels: 90°, 180°) and Session (2 levels: Baseline, Post

[2] We also ran the following analyses on tolerances of 10°, 15° and 30°. The results of the analyses were all the same, and the only difference was a main effect of tolerance (a tighter tolerance produces lower numbers across all conditions). We report the 20° analyses solely because this was a sensible range to assess both trained and untrained performance at 90° mean relative phase.

Training) as within subject factors. There was a significant interaction between Phase and Session ($F(1,6) = 15.4$, $p<.05$). No other effects were significant. To probe this interaction, we performed two-tailed, paired, t-tests comparing Baseline and Post Training thresholds separately for 90° and 180°. There was a significant difference between thresholds for Baseline vs. Post Training at 90° ($t(5) = 4.2$, $p < 0.01$) but not for 180° ($p>0.05$). Thresholds at 90° improved from Baseline (23.7°, SD=7.8°) to Post Training (12.3°, SD=3.2°) to be the same as at 180° with training, with no change at 180° (average threshold 11.4°, SD = 5.9°).

We also performed a repeated measures ANOVA on the 90° thresholds from the Experimental group with Session (6 levels: Baseline, each of the 4 training levels, Post Training) as a within subject factor (Figure 2). Training thresholds were computed from the data in the best (generally the last) session at a given feedback range. There was a significant main effect of Session ($F(5,28) = 3.0$, $p<.05$). The perceptual training was therefore successful. At the start of training, participants were unable to discriminate differences in relative phase between 65° and 115°, i.e. these would all equally be identified as 90°. After training, this interval was only from 80° to 100°. (Recall, we tested threshold both below and above 90° and the thresholds were the same.)

2. Movement (Figure 3): We performed a repeated measures ANOVA on the median proportion time on task with the tolerance set to 20°. There were two within subject factors, Phase (3 levels: 0°, 90° and 180°) and Session (3 levels: Baseline, Post Training and Retention). There was one between subjects factor, Group (2 levels: Experimental, Control). We predicted a three way Phase x Session x Group interaction, in which movement stability improved for the Experimental group at 90° only after training.

There was a significant main effect of Phase ($F(2,20) = 52.5$, $p<.01$) and Session ($F(2,20) = 4.9$, $p<.05$) but these were modified by the predicted Phase x Session x Group interaction ($F(4,40) = 4.8$, $p<.01$). No other effects were significant. Only participants in the Experimental group improved their movement stability across sessions, and this improvement was restricted to 90°. Control performance remained the same across sessions, and was identical to Baseline performance in the Experimental group. We confirmed this interpretation with two separate repeated measures ANOVAs for each group. The Experimental group showed a main effect of Phase ($F(2,10) = 29.4$, $p<.01$) and an interaction between Session and Phase ($F(4,20) = 5.5$, $p<.01$), while the Control group showed only a main effect of Phase ($F(2,10) = 24.8$, $p<.01$).

General Discussion

A key part to any perception-action account is an account of the learning process. Attention, in E. J. Gibson's (1969) terminology, requires education – a perceiver-actor must learn to become sensitive to information that specifies functionally relevant parts of the world. But learning is not just perceptual – learning also entails assembling the action part of the perception-action system, and integrating the perception and action components into a whole, functional, task-specific device (Bingham, 1988). Six participants were trained to improve their perceptual resolution of 90°, and we measured the effect on their movement stability at 90° and 180°. Overall, the participants improved in the perception task, and this translated to improved movement stability at 90° but not at 180°, without further practice of the movement task. As shown by the Control group, there was no significant improvement at movement stability at 90° in the absence of perceptual training.

Initial performance in the Choose 90° task was poor (with high thresholds) and erratic (high between subject variability). This erratic initial performance was not unexpected – previous judgment studies (e.g. Wilson et al.., 2003; Zaal et al.., 2000) have shown that discrimination of 90° is poor, which causes the variability of the judgments of both the mean relative phase and the variability around that mean to be at ceiling. The HKB model describes this in terms of attractors. The purpose of an attractor in a model is to account for a particular structure to behavior in that region of the state space. But attractors are not explanatory, they are descriptive. 0° is not stable because there is an attractor there – there is an attractor there because 0° is stable. The question is therefore, why is there an attractor *here*, rather than *there*? The perceptual judgment data (Bingham et al.., 1999, 2000; Zaal et al.., 2001) suggested that the reason is that people have poor access to the requisite information at 90°, better access at 180° and best access at 0°. The advantage in moving to this account is that we could now experimentally investigate the information in a way one cannot investigate an attractor. As we see in the current data, improving access to the information at a location allows behaviour to become structured at that location (i.e. an attractor forms). We demonstrated this here with the Post Training Choose 90° performance – thresholds come down and performance also became qualitatively more consistent across participants. This then led to stable movement, i.e. the formation of an attractor there.

But this is not a case of learning generalising across domains. Perception and action make a single domain – perception-action – and the training has had an effect on the overall system. This account follows recent modelling (e.g. Bingham 2001, 2004a, 2004b) and experimental (Wilson & Bingham, 2008) work that explicitly treats both informational and action components as identifiable elements in an overall task dynamic. This goes beyond the phenomenological, descriptive approach motivated by the HKB model and allows theoretical and empirical investigations of the composition and organisation of the dynamic that is creating the phenomena.

The current data demonstrate a second example of this. Performance in the Choose 180° task was already more stable than 90° within and between participants, reflecting the fact that 180° is already a stable location in the state space. There was no improvement in performance post-training in the Choose 180° or the movement task at 180°. Learning at 90° did not transfer to 180°, suggesting that what was learned during training is not available or is not used at 180°. This result is explained by the findings of Wilson & Bingham (2008), who took participants who had been trained on the judgment task and systematically perturbed candidate information variables (relative position, speed and frequency). Trained performance at 90° was primarily affected by perturbations of relative position (and to some extent relative frequency), while none of these perturbations had any effect at all on performance at 180°. The conclusion was that training at 90° had led participants to learn to use a novel information variable (involving position) to perform their judgments at 90° and only 90°. This information based account explains the lack of generalisation in that and the current studies in the same way as it explains generalisation of learning to symmetry partners seen in Zanone and Kelso (1992a, b). What defines the task space is information, and the system's behaviour follows this definition. It is not clear from the current data where, besides 90° this novel information variable is used. More experiments are planned to probe the space in more detail (training relative phases of, for instance, 45° or 135° and probing over a wider range).

In the current experiment, the improvement in movement stability at 90° occurred in the Post-Training session and persisted in the Retention session with no additional training. In an early version of this experiment (Wilson, 2005) the improvement was not detected until Retention. This quite surprising result was discussed at the time in terms of consolidation (Brashers-Krug, Shadmehr, & Bizzi, 1996; Faugloie, Bardy & Stoffregen, 2006; Karni, Meyer, Rey-Hipolito, Jezzard, Adams, Turner, & Ungerleider, 1998) with the suggestion that the new information variable that had been learned needed to be used in service of an action to complete the perception-action learning process. The current results suggest this may not be entirely correct. The main difference between the current and earlier experiments that we suspect made the difference was the amount of training, which was significantly more extensive in the current experiment. Still, the consolidation phenomenon was quite robust across participants in the previous study, and it remains to explicitly manipulate the amount of training to investigate this further.

In the current experiment, participants improved their movement stability at 90° following training to improve their perceptual ability at 90°. This result provides strong support for the hypothesis that movement stability is a function of perceptual ability. Perception-action systems are *systems*, and the composition and organisation of the motor as well as the informational components contributes to the system's overall behaviour.

Table 1

Number of training sessions at each feedback tolerance level

Participant	Training Threshold				Total
	+/-40°	+/-30°	+/20°	+/10°	
1	1	4	3	4	**12**
2	1	2	4	4	**11**
3	1	1	1	4	**7**
4	2	2	4	6	**14**
5	1	2	3	6	**12**
6	2	2	2	1	**7**

Table 1. Number of training sessions for each participant at each level of error tolerance.

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Figure Captions

Figure 1. Schematic diagram of the movement task set up. The judgment displays used identical visual stimuli without the joystick.

Figure 2. Mean thresholds (in degrees and with standard error bars) for judgments made by the Experimental group at Baseline, during Training at each of the four sets of intervals tested and at Post Training. Thresholds and standard errors at 90° came down significantly with training. Note that Baseline and Post Training reflect performance in the absence of feedback.

Figure 3. ‘Proportion time on task’ data for the Experimental vs. Control groups performing 0°, 90° and 180° across three Assessment sessions (filled diamonds: Baseline; open squares; Post Training; open triangles: Retention). This number is the proportion of time spent within an error bandwidth (set to 20°) from the target relative phase and measures both movement stability and mean performance in a single number. Control performance did not change across sessions, while the perceptual training lead to a significant improvement in movement stability at (only) 90° for the Experimental group.

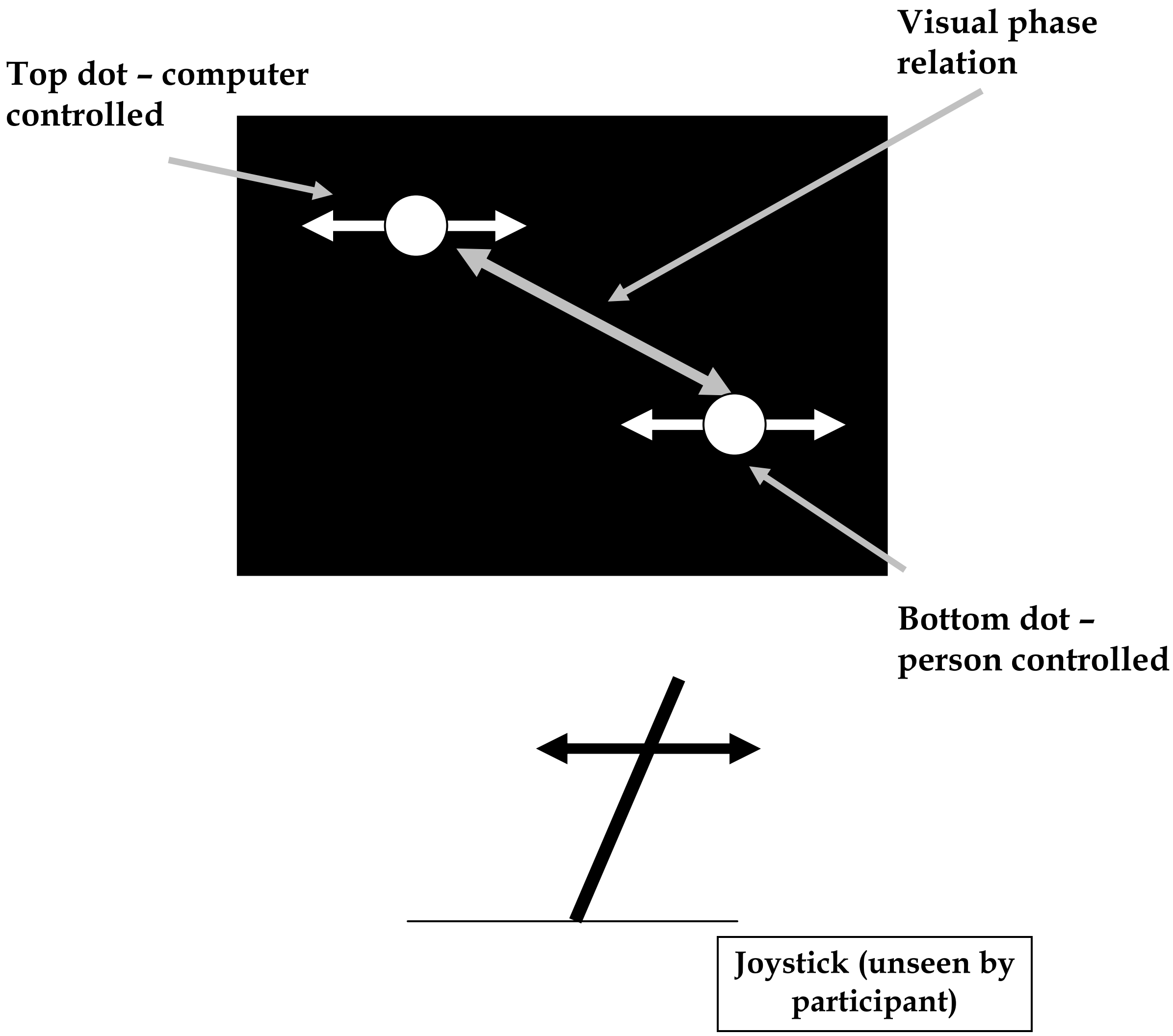
Visual phase relation
Top dot – computer controlled
Bottom dot – person controlled
Joystick (unseen by participant)

Figure 1

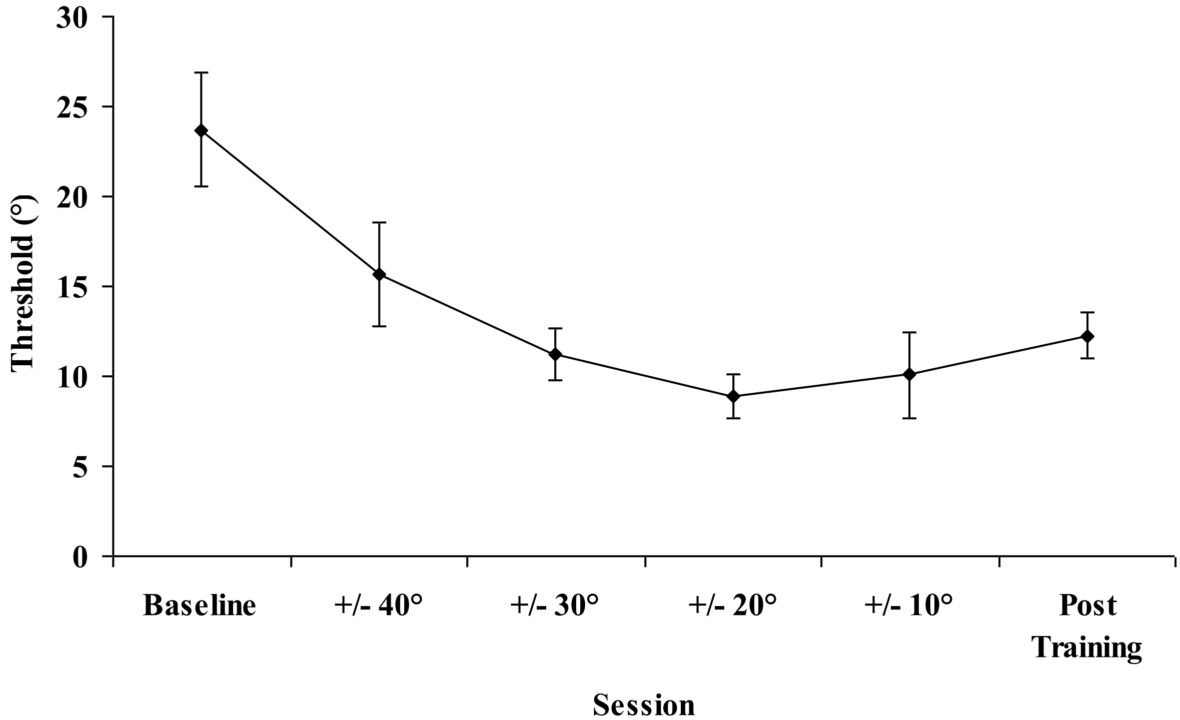
30
25
20
15
10
5
0
Threshold (°)
Baseline
+/- 40°
+/- 30°
+/- 20°
+/- 10°
Post Training
Session

Figure 2

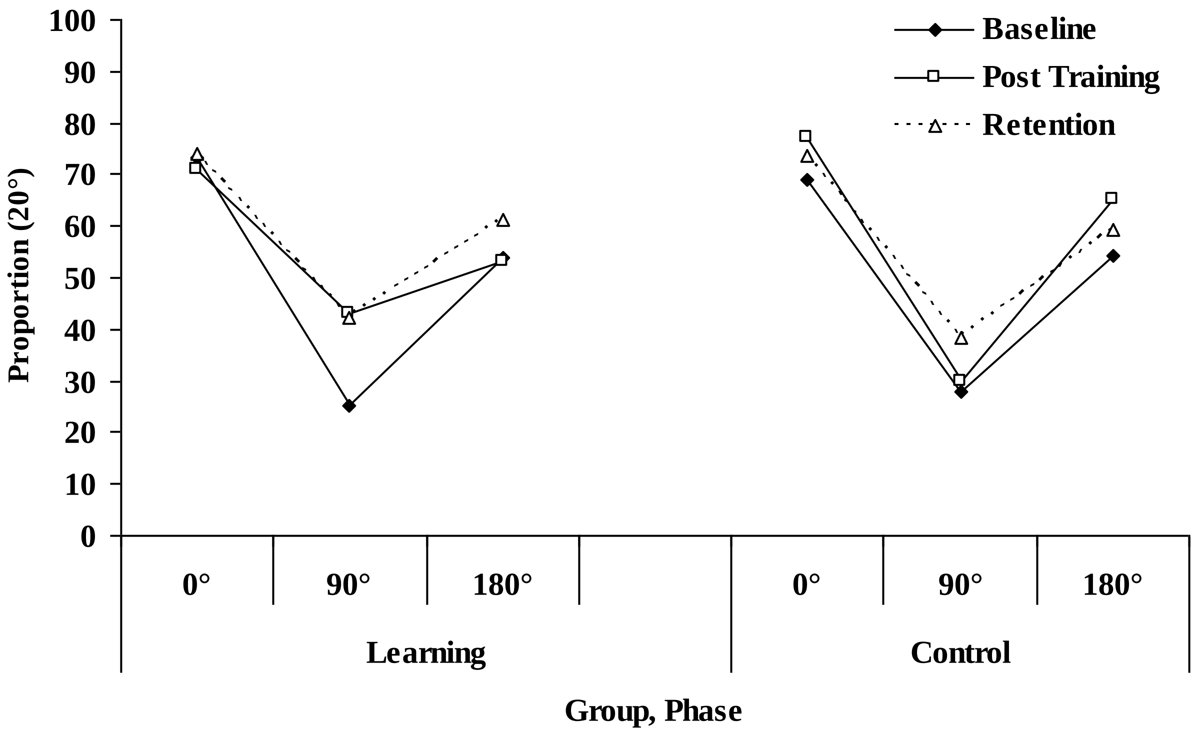
100
90
80
70
60
50
40
30
20
10
0
Proportion (20°)
Baseline
Post Training
Retention
0°
90°
180°
0°
90°
180°
Learning
Control
Group, Phase

Figure 3