Separate representations of dynamics in rhythmic and discrete movements:
Evidence from motor learning

Running Head: Separate representations of rhythmic and discrete movements

Authors and author addresses:

Ian S. Howard
Computational and Biological Learning Laboratory,
Department of Engineering,
University of Cambridge,
Trumpington Street,
Cambridge CB2 1PZ, UK.
Email: ish22@cam.ac.uk

James N. Ingram
Computational and Biological Learning Laboratory,
Department of Engineering,
University of Cambridge,
Trumpington Street,
Cambridge CB2 1PZ, UK.
Email: jni20@cam.ac.uk

Daniel M. Wolpert
Computational and Biological Learning Laboratory,
Department of Engineering,
University of Cambridge,
Trumpington Street,
Cambridge CB2 1PZ, UK.
Email: wolpert@eng.cam.ac.uk

Corresponding author:
Ian S. Howard
Computational and Biological Learning Laboratory,
Department of Engineering,
University of Cambridge,
Trumpington Street,
Cambridge CB2 1PZ, UK.
Email: ish22@cam.ac.uk
Separate representations of dynamics in rhythmic and discrete movements:

Evidence from motor learning

Ian S. Howard, James N. Ingram and Daniel M. Wolpert
Computational and Biological Learning Lab, Department of Engineering,
University of Cambridge, Trumpington Street, Cambridge CB2 1PZ, UK.

Five Keywords: motor learning, interference, rhythmic movements, discrete movements, human

Abstract

Rhythmic and discrete arm movements occur ubiquitously in everyday life and there is a debate as to whether these two classes of movements arise from the same or different underlying neural mechanisms. Here we examine interference in a motor learning paradigm to test whether rhythmic and discrete movements employ at least partially separate neural representations. Subjects were required to make circular movements of their right hand while they were exposed to a velocity-dependent force-field that perturbed the circularity of the movement path. The direction of the force-field perturbation reversed at the end of each block of 20 revolutions. When subjects made only rhythmic or only discrete circular movements, interference was observed when switching between the two opposing force-fields. However, when subjects alternated between blocks of rhythmic and discrete movements, such that each was uniquely associated with one of the perturbation directions, interference was significantly reduced. Only in this case did subjects learn to co-represent the two
opposing perturbations, suggesting different neural resources were employed for the
two movement types. Our results provide further evidence that rhythmic and discrete
movements employ at least partially separate control mechanisms in the motor
system.

Introduction

During everyday life, we move our arms using rhythmic or discrete movements, or a
combination of both, depending on the task. For example, to brush our teeth or beat
and egg we use rhythmic movements, whereas to catch a ball or grasp a cup we use
discrete movements. The relationship between these two classes of movements has
been the topic of many studies (Buchanan et al. 2006; Ikegami et al. 2010; Miall and
Ivry 2004; Schaal et al. 2004; Smits-Engelsman et al. 2002; Sternad 2000; Sternad
and Dean 2003; van Mourik and Beek 2004). One view is that discrete movements
represent the fundamental class and that rhythmic movements are merely a
concatenation of a series of discrete movements. The opposing view is that rhythmic
movements represent the fundamental class and that discrete movements are simply
truncated rhythmic movements. Both of these viewpoints would suggest that only a
single control mechanism is involved. A third viewpoint is that rhythmic and discrete
movements represent two distinct movement classes that are mediated by separate
neural control circuitry. Further support for this latter hypothesis has recently been
obtained from behavioral (Ikegami et al. 2010) and imaging studies (Schaal et al.
2004).
Behavioral studies of motor adaptation to perturbations that examine interference and transfer provide a means to investigate the underlying partitioning of neural representations and control mechanisms. These studies typically use two different perturbations which show interference in the absence of contextual cues (Bock et al. 2001; Brashers-Krug et al. 1996; Goedert and Willingham 2002; Karniel and Mussa-Ivaldi 2002; Krakauer et al. 2005; Krakauer et al. 1999; Miall et al. 2004; Shadmehr and Brashers-Krug 1997; Wigmore et al. 2002). When the perturbations are each associated with a different context, a reduction in this interference is often observed.

In the case of discrete movements, several studies have shown a reduction in interference when each perturbation is associated with a unique context (Cothros et al. 2009; Howard et al. 2008; 2010; Krouchev and Kalaska 2003; Nozaki et al. 2006).

Several recent models have been developed to account for the reduction in interference observed in the presence of contextual cues (Lee and Schweighofer 2009; Nozaki and Scott 2009). These models propose multiple internal representations which can be selectively engaged by different contexts (Wolpert and Kawato 1998).

In the current study we ask whether rhythmic and discrete movement classes are associated with separate representations. At a neurophysiological level, context-dependent learning of opposing perturbations may involve different populations of neurons which are engaged by the different sensorimotor contexts (Nozaki et al. 2006). Similarly, when the perturbation remains constant, a lack of transfer from one context to another may imply some separation of the underlying representations.

With regards to rhythmic and discrete movements, Ikegami investigated transfer during motor learning of a visuomotor perturbation during point-to-point movements.
They found incomplete transfer from rhythmic to discrete movements suggesting that these two classes of movements may engage separate representations. Here we use a dynamic interference paradigm to investigate the representations associated with rhythmic circular and discrete circular movements. Specifically, subjects performed continuous circular movements consisting of multiple revolutions in the rhythmic case or discrete movements consisting of one and a quarter revolutions in the discrete case. We first verify that subjects adapt similarly to the dynamic perturbation for each movement class and that interference occurs when the perturbation direction is reversed. We then show that interference is reduced in a switching paradigm when each perturbation direction is associated with a different movement class. These results provide further evidence that rhythmic and discrete movements are distinct classes that engage at least partially separate neural representations.

**Materials and Methods**

A total of 44 right-handed subjects took part in the study (2 were excluded from the final analysis as described below). Subjects provided written informed consent and were naïve to the aims of the experiment. The protocol was approved by a local ethics committee and all subjects completed an Edinburgh handedness questionnaire.

All experiments were performed using a vBOT planar robotic manipulandum, with associated virtual reality C-rig and air table (Howard et al. 2009). The vBOT is a custom-built back-drivable planar robotic manipulandum which exhibits low-mass at its handle. Position is measured using optical encoders sampled at 1000 Hz and torque...
motors allow translational forces to be applied at the same rate. A virtual reality system was used to overlay target and cursor images in the plane of movement. Subjects were seated in a sturdy chair in front of the apparatus. They were firmly strapped against the backrest of the chair using a four-point seatbelt to reduce body movement. They held the robot handle in their right hand and their right forearm was supported by an air sled which constrained movements to the horizontal plane. Subjects were prevented from viewing their hand directly.

All experiments required subjects to perform either rhythmic or discrete clockwise circular movements around the circumference of a visually presented target circle (8 cm radius). The centre of the target circle was located in the subject’s mid-sagittal plane approximately 30 cm below the eyes and 30 cm in front of the chest. The handle controlled a red cursor (disc of 0.5 cm radius). At the start of each trial, the target circle and the start position for the movement appeared. The start position was a 1.0 cm radius disc located on the target circle’s circumference. At the start of each trial the vBOT applied a force to the subject’s hand, moving the cursor to the start position. A trial began when the cursor had remained within its start position at a speed below 0.1 cm/s for 0.5 s. Subjects were then cued to start the movement by an acoustic tone which was used as a go signal. They were required to achieve the circular movement at a speed of 1 revolution per second. To assist this, a pair of visual indicators (pacing cursors) moved along the circumference of the target circle at the required frequency. These were short line segments perpendicular to the tangent, similar to the distal parts of the hands of a clock and separated by 180°. Subjects were informed that the moving cursors were only meant to act as a pacemaker for the speed of their movements and that they were not required to track
them. To this end, a pair of pacing cursors (rather than a single cursor) was used to make it easier for subjects to pace their movement around the circle. Notably, using a pair of cursors discouraged subjects from tracking a single cursor. The cursors were present in both the discrete and rhythmic conditions.

**Rhythmic and discrete movements**

Subjects performed either continuous circular movements consisting of 20 revolutions in the rhythmic case or discrete movements consisting of $1\frac{1}{4}$ revolutions in the discrete case. They performed blocks containing either a single rhythmic movement (1 x 20 revolutions) or 16 individual discrete movements ($16 \times 1\frac{1}{4} = 20$ revolutions).

For rhythmic movements the start position was always located at 12 o’clock on the circumference of the target circle. Subjects were required to make 20 revolutions continuously, without stopping in-between. The experimental algorithm counted the number of revolutions and terminated the trial after 20 had been performed. For discrete movements, subjects were required to make single discrete circular movements of $1\frac{1}{4}$ revolutions per trial, with a short pause (approximately 6 sec) between each trial. The start and end position for the movement were displayed on the circumference of the target circle. Specifically, at the beginning of each trial, the start position was displayed. After the movement had been initiated, the start position disappeared and was replaced by the end position ($1\frac{1}{4}$ revolutions clockwise relative to the start position). The end position then became the start position for the next trial.

At the beginning of each block, the start position was located at 12 o’clock (as for the rhythmic case), stepping $\frac{1}{4}$ revolution increments around the target circle with each consecutive trial. Consequently, after 16 discrete movements, the end position
coincided with the start position for the block. For both rhythmic and discrete cases, the subject’s performance was monitored and error messages were displayed if too many or too few rotations were performed. Subjects were also warned if their movements were too slow.

**Perturbation**

Each block of movements was either made in a Null field (no forces) or with the vBOT generating one of two possible dynamic perturbations which consisted of a viscous skew field (Shadmehr and Mussa-Ivaldi 1994):

\[
\begin{bmatrix}
F_x \\
F_y
\end{bmatrix} = k \begin{bmatrix}
1 \\
0
\end{bmatrix} \begin{bmatrix}
\dot{x} \\
\dot{y}
\end{bmatrix}
\]

(1)

where \(k\) was set equal to \(-8.5\) N m\(^{-1}\) s (perturbation P1) or \(+8.5\) N m\(^{-1}\) s (perturbation P2). The perturbations P1 and P2 are illustrated in Figure 1A & B, respectively.

**Catch trials and catch revolutions**

In general there are two ways of adapting to a state-dependent force field. First, subjects can simply co-contract the muscles, thereby stiffening the arm so that the positional displacement due to the experienced forces are reduced. Such a mechanism works for any force-field and does not require the motor system to represent the particular structure of the field. Second, the subject can learn a mapping between the state of the limb and the force required to compensate for the force-field. Such learning is specific for the particular field. Indeed, previous studies have suggested
that during exposure to a dynamic force-field, it is not a virtual trajectory that is
learned, but rather a mapping from state to expected force; that is, a controller
(Conditt et al. 1997). Co-contraction and specific compensation are not mutually
exclusive and a number of studies have examined their interaction, (Tee et al. 2010).
Our use of catch trials to distinguish between adaptation due to non-specific co-
contraction and adaptation due to specific compensation to the state-dependent force-
field is based on the standard method (Shadmehr and Mussa-Ivaldi 1994). To examine
these components in our experiments, catch trials were used to examine the after-
effects observed when the field was unexpectedly turned off. In this case, the two
strategies lead to different predictions with respect to the presence of after-effects. If
subjects use stiffness, then no after-effects should be seen. Specifically, in the absence
of the force-field, subjects simply make the normal movement with a stiffer arm.
However, if specific compensation is used, subjects will initially produce a force
which is inappropriate in the absence of the force-field, causing the hand to deviate
from the intended movement.

In the case of discrete movements, we included randomly presented catch trials in
which the force field was turned off for an entire trial. In the case of rhythmic
movements, one of the multiple revolutions was used to assess learning and we refer
to this as a catch revolution. During such a rhythmic movement catch revolution, the
force was rapidly ramped down (over 100 ms) to zero for one revolution and then
ramped up again. Ramping the forces in this manner avoided force discontinuities.

Error measures
Because subjects were asked to make circular movements, performance on each trial was defined with respect to the circularity of the hand path. The skew fields used for perturbations P1 and P2 have the effect of causing circular movements to deform into elliptical paths (see example in Figure 2B). To analyze the paths, we used an algorithm that can reliably operate on scattered data to fit an ellipse (Fitzgibbon et al. 1999). We then define an error measure that is given by the ratio of the long axis to the short axis of the ellipse, from which unity is subtracted. The direction of the tilt induced by the perturbation is then captured by the sign of the angle of the long axis relative to vertical, with a clockwise rotation taken as positive (Figure 1C & D). We refer to this measure as the signed error.

\[ \text{SignedError} = \text{Sign}(\theta) \left( \frac{b}{a} - 1 \right) \]  

To quantify performance, we calculated the signed error over each entire block excluding data from catch trials (or revolutions) and points when the hand speed was less than 10 cm s\(^{-1}\). For the discrete trails, the last 25% of data points of each trial was also excluded (to exclude terminal corrective movement to reach the final target position). Catch trials and catch revolutions were analyzed separately in the same way.

**Statistical analysis**

We perform only hypothesis-based planned comparisons and use repeated measures ANOVA, which corresponds to a two-tailed t-test. We report uncorrected p-values.
across subjects to determine statistical significance of signed error. Although we perform a number of tests overall, only a few are truly critical for the conclusions of the paper and these are in Experiment 5 where we examine the post-exposure after-effects.

Experiment 1: Static movement class – rhythmic

The purpose of Experiment 1 was to confirm that subjects could learn the velocity-dependent force-fields whilst making rhythmic circular movements. The experiment is illustrated in Figure 2A. A total of 7 subjects participated in this experiment. However, one subject was excluded because of failure to produce consistent angular speed profiles across the trials, leaving 6 subjects in the final analysis (n=6). The experiment included 60 blocks of rhythmic movements. The experiment consisted of an initial pre-exposure phase of two blocks in the Null field (no forces), two consecutive exposure phases of 28 blocks each, and a final post-exposure phase of two blocks again in the Null field.

Half the subjects (n=3) experienced viscous skew field P1 for the first exposure phase and viscous skew field P2 for the second exposure phase. For the other half of the subjects (n=3), the order was reversed. This procedure was adopted to counterbalance any directional effects that may arise due to interaction with the biomechanics of the arm and to minimize any other effects of direction. During the last four blocks of each exposure phase, a single catch revolution was included pseudo-randomly between the 12th and 18th revolution.
Experiment 2: Static movement class – discrete

The purpose of Experiment 2 was to confirm that subjects could learn the velocity-dependent force-fields whilst making discrete circular movements. A total of 6 subjects (n=6) participated. The experiment was identical to Experiment 1, except that subjects made discrete circular movements (Figure 3A). In this case, each block consisted of 16 discrete trials, with each trial consisting of a circular movement of $1^{1/4}$ revolutions. During the last four blocks of each exposure phase, catch trials (Null field trials) were included and were pseudo-randomly inserted between the 10th and 14th trials in each block.

Experiments 3-5: Switching perturbation

In Experiments 3-5 we used an interference paradigm to determine if rhythmic and discrete movements involve separate control mechanisms. A total of 6 subjects participated. Subjects were exposed to opposing perturbations which alternated across consecutive blocks so that odd numbered blocks were associated with one perturbation direction and even numbered blocks with the other (Figure 4). In the first two experiments, subjects made either rhythmic movements (Experiment 3, Figure 4A) or discrete movements (Experiment 4, Figure 4B) while the perturbations alternated. In these experiments the class of movement remained static throughout. In Experiment 5, subjects made rhythmic and discrete movements alternately across consecutive blocks so that each perturbation direction was associated with a different movement class (Figure 4C).
Experiment 3: Switching perturbation, static movement class – rhythmic

In Experiment 3, 6 subjects (n=6) performed 90 blocks of rhythmic movements (Figure 4A). The experiment began with a pre-exposure phase consisting of two blocks in the Null field, followed by an exposure phase of 86 blocks in which subjects experienced the alternating dynamic viscous skew field perturbations (P1 and P2, see Figure 1A & B). Finally, subjects performed a post-exposure phase consisting of two blocks in the Null condition. As in Experiment 1, catch revolutions were included to assess learning during the last 4 exposure blocks.

Experiment 4: Switching perturbation, static movement class – discrete

Experiment 4 was identical to Experiment 3, except that 6 subjects (n=6) made 16 discrete movements per block, and catch trials were used to assess learning (Figure 4B).

Experiment 5: Switching perturbation and movement class – rhythmic / discrete

Experiment 5 was identical to Experiment 3, except that subjects made rhythmic and discrete movements alternately across consecutive blocks (Figure 4C). A total of 7 subjects participated in this experiment. However, one subject was excluded because cursor movements made during the initial exposure block lied outside the normal workspace. For the 6 remaining subjects (n=6), the perturbation direction was counter-balanced, so that half the subjects (n=3) experienced perturbation P1 for odd-
numbered blocks and perturbation P2 for even-numbered blocks. For the other half of the subjects (n=3), the order was reversed.

Experiments 3-5: Analysis

We performed an analysis which allowed us to compare both the static movement experiments, which consisted of 90 blocks for each of the two movement classes, with the switching movement experiment, which consisted of 45 blocks for each of the two movement classes. Specifically, for the two static movement experiments we computed the mean signed error over pairs of blocks, reducing the error time series from 90 blocks to 45 block pairs, one for each static movement class (rhythmic and discrete). In this case, the sign of the error was adjusted to take into account the opposite perturbation directions associated with consecutive blocks. For the switching experiment, the signed error was computed separately for the blocks associated with each movement class. This yielded two time series consisting of 45 blocks, one for each switching movement class. When calculating the average across subjects, we also adjusted the sign of the error according to the perturbation direction (which was counterbalanced across subjects as described above).

Control experiments

In the previous experiments, subjects were allowed to make movements without having to track the cursors, which were present simply to pace movement speed. A comparison of the discrete and the rhythmic movement speeds showed that they had
slightly different ranges. To ensure that any effects from Experiment 5 did not arise due to these small differences in speed, two control experiments were performed.

**Experiment S1: Switching perturbation and movement class – speed control**

The control Experiments S1 (see Supplementary Material) was similar to Experiment 5, except that a modified pacing cursor was employed so as to ensure a closer match in speed.

**Experiment 6: Switching perturbation, static movement class – two-speed control**

Experiment 6 was a control experiment similar to Experiment 3, except that subjects (n=6) were required to make rhythmic movements that alternated across successive blocks between rotational frequencies of 0.9 Hz and 1.1 Hz. The speed differences were chosen to be roughly equivalent to the difference that we observed between the rhythmic and discrete cases in Experiment 5, in order to investigate if such speed differences were sufficient to account for the observed learning (the speed profiles for these rhythmic and discrete cases from Experiment 5 are shown in Figure S2 in the Supplementary Material). As such, each perturbation direction was associated with rhythmic movements of a different frequency. This is in contrast to Experiment 3 in which subjects made rhythmic movements at 1 Hz for both perturbations. To compensate for the reduction in speed between the two conditions, the field strength was increased at the lower rotational frequency and decreased at the higher rotational frequency. Specifically, viscous skew fields P1 and P2 employed gains of $k=-7.64 \text{ N m}^{-1} \text{s}$ and $k=+9.33 \text{ N m}^{-1} \text{s}$, respectively (Equation 1). Histograms of hand velocity and
position, as well as the mean and standard error of the speed profiles across subjects, were computed separately for the two rhythmic frequencies.

Results

Static movement class experiments

In the first two experiments, subjects carried out a single movement class (either rhythmic or discrete) throughout the duration of each experiment. They experienced a viscous skew field in one direction for the first half of the experiment and in the opposite direction for the second half. To quantify performance, we used a measure of circularity in which larger magnitude values corresponded to more elliptical movements and the sign reflected the direction of the tilt of the long axis (see Methods and Figure 1C & D).

Experiment 1: Static movement class – rhythmic

Figure 2B shows the paths for a representative subject at key stages of the experiment and Figure 2C shows the signed error as a function of block, averaged across all subjects. During the pre-exposure phase, subjects made roughly circular movements characterized by a low error. Upon introduction of the first perturbation the movement paths became elliptical due to the compressive and expansive nature of the field and the error increased correspondingly. Over the course of the 28 exposure blocks the movements became more circular and performance improved significantly (change in error from first to last exposure block $+0.32\pm0.08$, p=0.009). The next 28 blocks were
performed with the opposite perturbation direction which resulted in a change in the
sign of the error (Figure 2C). Immediately after the change in the perturbation, the
magnitude of the error increased. As before performance improved over the course of
exposure (-0.47±0.1, p=0.01). The magnitude of the error on the first block in the
new perturbation was significantly larger than the corresponding block in the first
perturbation (0.31±0.09 higher, p=0.02). This suggests that there is anterograde
interference between the two perturbations for rhythmic circular movements,
consistent with previous studies showing interference during point-to-point
movements (Shadmehr and Brashers-Krug 1997).

To examine whether the reduction in error could have arisen solely from co-
contraction we used catch revolutions, in which the perturbation was transiently
turned off for a single revolution chosen randomly during the last 4 blocks of each
perturbation. During the catch revolutions (Figure 2C mauve circles), the errors were
in the opposite direction to the perturbation and were significantly different from
zero for the first (mean 0.63±0.07, p<0.001) and second (mean -0.36±0.07, p=0.004)
perturbations. These results suggest that subjects were specifically compensating for
the each particular perturbation.

**Experiment 2: Static movement class – discrete**

The second experiment was identical to the first except that subjects made discrete
movements throughout. Figure 3B shows the paths for a representative subject and
Figure 3C shows the signed error as a function of block, averaged across all subjects.
The features in these plots are similar to the first experiment. Upon introduction of the
first perturbation the movement paths became elliptical due to the compressive and expansive nature of the field and the error increased correspondingly. Over the course of the 28 exposure blocks the movements became more circular and performance improved significantly (change in error from first to last exposure block $+0.28\pm0.06$, $p=0.004$). The next 28 blocks were performed with the opposite perturbation direction which resulted in a change in the sign of the error (Figure 3C). Immediately after the change in the perturbation, the magnitude of the error increased. However, as before performance improved over the course of exposure ($-0.53\pm0.11$, $p=0.006$). The magnitude of the error on the first block in the new perturbation was significantly larger than the corresponding block in the first perturbation ($0.26\pm0.09$ higher, $p=0.04$). This suggests that there is anterograde interference between the two perturbations for discrete circular movements. As with the first experiment, random catch trials were presented during the last 4 blocks of each perturbation. Catch trial errors (Figure 3C mauve circles) were significantly different from zero for both the first (mean=$0.59\pm0.09$, $p=0.002$) and second (mean=$-0.46\pm0.06$, $p<0.001$) perturbations, suggesting that subjects were specifically compensating rather than co-contracting.

**Experiments 3-5: Switching perturbation**

Experiments 3-5 constitute the main results from the current study. They were run to determine if interference between opposing perturbations would be reduced by associating each perturbation with a different movement class. This would suggest that the control mechanisms associated with each movement class were at least partially separate. In these experiments, subjects were exposed to switching...
perturbations (P1 and P2) in which the perturbation direction alternated across successive blocks (Figure 4).

Figure 5A-C shows the movement paths for representative subjects at key stages for the three experiments (the two static movement class experiments and the switching movement class experiment). Following the color code from Figure 4, the paths from odd blocks are plotted in red and the paths from even blocks are plotted in blue. Figure 5D shows the signed error for all three experiments. Note that the signed error for the four experimental conditions is plotted with an arbitrary sign to facilitate the presentation. Each condition generated errors in both directions (as within each experiment the field directions were counterbalanced) and these were combined in an appropriate fashion (see Methods).

During the pre-exposure phase in the Null field of each experiment, subjects made roughly circular movements characterized by a low signed error (pre-exposure bar chart at left of Figure 5D; see figure legend for key to colors). Upon introduction of the perturbation, signed error increased. In Figure 5A-C, the errors are larger for one perturbation than the other due to the interaction of the biomechanical properties of the arm and the direction of the perturbation. The signed error reduced over the course of exposure in all cases, but with important differences between the static and switching cases, which are described in detail below.

Experiment 3: Switching perturbation, static movement class – rhythmic
In the static rhythmic experiment (Figure 5D, green curve) signed error decreased significantly between the first and last exposure block pairs (-0.28±0.06, p=0.005). The mean signed error during catch revolutions was also significantly greater than zero (0.24±0.03, p=0.0003). However, the signed error during the first post-exposure block (green bar on right of Figure 5D) was not significantly different from zero (-0.06±0.04, p=0.23). The results from post-exposure block suggest that the improvement in performance was dominated by co-contraction. However the catch revolutions indicate that some limited specific compensation was present within each block.

Experiment 4: Switching perturbation, static movement class – discrete

In the static discrete experiment (Figure 5D, blue curve) signed error also decreased significantly between the first and last exposure block pairs (0.12±0.05, p=0.05). However, in this case the mean signed error during catch trials was not significantly different from zero (-0.08±0.04, p=0.11). Similarly, the signed error during the first post-exposure block (blue bar on right of Figure 5D) did not differ significantly from zero (0.07±0.04, p=0.12). The results from catch trials and the post-exposure block suggest that the improvement in performance was due primarily to co-contraction with no evidence for the presence of specific compensation within each block.

Experiment 5: Switching perturbation and movement class – rhythmic / discrete

In the rhythmic blocks of the switching movement class experiment (Figure 5D, red curve) signed error decreased significantly between the first and last exposure blocks
The mean signed error during catch revolutions was negative and significantly different from zero \((-0.358\pm0.1, p=0.02)\). In addition, the signed error during the post-exposure block (red bar on right of Figure 5D) was also negative and significantly different from zero \((-0.12\pm0.01, p<0.001)\). A similar pattern was observed for the discrete movement blocks of this experiment (Figure 5D, grey curve). Specifically, signed error decreased significantly between the first and last exposure blocks \((0.30\pm0.11, p=0.047)\). The mean signed error during catch trials \((0.30\pm0.06, p=0.004)\) and during the post-exposure block (grey bar on right of Figure 5F, \(0.12\pm0.02, p=0.003\)) were both positive and significantly different from zero. Importantly, these “after-effects” were in the opposite direction to the errors due to the perturbations. Thus, in contrast to the static movement class experiments (3 & 4, described above), the significant post-exposure “affect-effects” suggest that the improvement in performance in this case was due to specific compensation for the perturbations associated with each movement class. This is consistent with partially separate control mechanisms for rhythmic and discrete movements which would allow the partitioning of perturbation-specific learning for each movement class.

*Control experiments*

It is possible that the improvement in performance observed for the switching movement class experiment (Experiment 5, above) may have resulted from differences in the kinematics between the rhythmic and discrete movements rather than differences in the underlying control mechanisms. Two control experiments were therefore performed to examine whether such kinematic differences could explain the results.
Experiment S1 (See Supplementary Material) was identical to Experiment 5, except that the speed at which subjects made the circular movements was more strictly controlled. Results show that this did not affect the degree of adaptation in the switching condition (Figure S3).

Experiment 6: Switching perturbation, static movement class – two-speed control

Experiment 6 was an additional control experiment to examine the effects of differences in speed on the ability to learn the opposing perturbations. In this case, rather than associating each perturbation direction with a different movement class (as in the original Experiment 5), each was associated with a different speed of rhythmic rotation (1.1 Hz and 0.9 Hz). These values were chosen to correspond to values observed during Experiment 5, and the differences were perceived as quite substantial by the subjects (see Methods for further detail). Figure 6A and B show the velocity and position distributions, respectively, for this experiment. The different speeds of rotation can be clearly seen in the velocity distribution plots (Figure 6A), whereas the position distributions are quite similar (Figure 6B). This can also be appreciated in the mean speed profiles, which are shown in Figure 6C (red=1.1 Hz, blue=0.9 Hz). We compared the average speed during the plateau regions between the two speed conditions across subjects and found a significant difference (8.2±1.1 cm/sec, p<0.001). Note that this speed difference is comparable to that observed between the rhythmic and discrete movement classes of the switching Experiment 5.
Figure 6D compares the signed error for the static rhythmic experiment (red; Experiment 3, above) with the two-speed control experiment (green). As can be seen, the plots are very similar for both experiments. Specifically, there were no significant differences for the final exposure errors between the two experiments (-0.03±0.05, p=0.54). Moreover, as for the original static rhythmic experiment, the signed error during the post exposure block did not different significantly from zero (-0.055±0.04, p=0.22). These results show that differences in rotational speed that were comparable to those observed in the switching movement class experiment were insufficient to allow subjects to co-represent the opposing perturbations.

**Discussion**

We used a motor learning interference paradigm to examine the representations involved in the control of rhythmic and discrete circular arm movements. For comparison with previous point-to-point reaching studies, we first confirmed the presence of anterograde interference when the direction of a dynamic force-field reversed, during either rhythmic or during discrete circular movements. We then examined a condition in which subjects were exposed to a dynamic force-field, whose direction reversed across successive blocks. In two experiments, subjects performed only rhythmic or only discrete movements while the perturbation direction reversed with each block. In both cases, performance improved over the course of the experiment, but Null-field catch and post-exposure trials suggested that this primarily arose through co-contraction rather than specific learning of the force fields. However, when each force-field direction was associated with a different movement class (either rhythmic or discrete) performance improved, with catch trials and post-
exposure after-effects demonstrating that subjects had learned to compensate specifically for the particular perturbation associated with each movement class. These results suggest that the control mechanisms for rhythmic and discrete movements are at least partially separate.

As pointed out by Hogan and Sternad (2007), in many previous studies the meanings of the terms rhythmic and discrete have not been defined precisely. To address this problem they have proposed rigorous taxonomic definitions to describe different classes of movement. Their definitions are mathematically precise, including several sub-classifications for both rhythmic and discrete movement types. They propose the key feature of discrete movements is that they consist of a movement between starting and ending postures (of the end-effector) with a static holding phase before and after the movement. In contrast, the term rhythmic is used to cover a wide range of cyclic or periodic movements. In particular, they subdivide rhythmic movements on the basis of the regularity of their periodicity, which range from strictly and almost periodic, through quasi- and transiently-periodic, to recurrent and repetitive movements. They note that repetitive discrete movements can also fall within the definition of rhythmic movements and these categories are not mutually exclusive. To further distinguish these classes, they also consider the smoothness of movement. Thus, whereas some repetitive discrete movements may be classed as rhythmic, they are often not as smooth as continuous rhythmic movements, since they include discontinuities (non-zero high order derivatives) in their movement paths introduced at their stopping and starting points.
In our study, we chose our two movement conditions to be distinct classes, as defined by Hogan and Sternad. Our discrete movements consisted of circular rotations between start and end positions, with a static holding phase of approximately 6 sec between each movement. In addition, the start and end positions changed between each movement, thus minimizing cyclic repetitions. In contrast, we chose our rhythmic movements to be multiple continuous rotations with no pauses between revolutions. These movements were smooth, and (almost) periodic (that is, as periodic as subjects were able to make) and consequently quite unlike repetitive discrete movements.

A recent study examined transfer of visuomotor learning between rhythmic and discrete movements (Ikegami et al. 2010). In one experiment, subjects were exposed to visuomotor perturbations whilst first performing either a set of discrete movements followed by a set of rhythmic movements or vice-versa. The study reports almost complete transfer of learning from discrete to rhythmic movements, but very little transfer from rhythmic to discrete movements, suggesting differences between the two movement classes. In a second experiment, multiple sets of rhythmic movements were performed in a visuomotor perturbation with delays between them. They found that at the beginning of each rhythmic movement from the second set onwards, errors were large for the first cycle, decreasing rapidly on subsequent cycles. In addition, when discrete training was employed with a large delay between trials, transfer to rhythmic movements was high for the first cycle, but then degraded for the next few cycles before subsequently improving again. They hypothesized that this implies the first cycle of the rhythmic movement engages control mechanisms associated with discrete movements. Overall, they draw the conclusion that different neural control
mechanisms are employed for rhythmic and discrete movements. The current study is
complementary to the Ikegami study in two ways. Firstly, we investigated the learning
of dynamic perturbations rather than kinematic transformations. Secondly, we used
interference to probe the representations associated with the two movement classes.
Thus, the current study supports the hypothesis made by Ikegami that different neural
control mechanisms are employed for rhythmic and discrete movements.

Previous studies have explored other contextual cues that allow opposing
derturbations to be concurrently represented and have focused on discrete point-to-
point movements (Cothros et al. 2009; Howard et al. 2008; 2010; Krouchev and
Kalaska 2003; Nozaki et al. 2006). For example, in the case of dynamics, with
extensive training, color can provide a contextual cue (Krouchev and Kalaska 2003).
In addition, it has been shown that subjects are able to switch between a dynamic
perturbation and a Null field on the basis of visual feedback relating to grasp (Cothros
et al. 2009). Another study showed that associating opposing perturbations with
unimanual and bimanual movements allowed subjects to concurrently represent the
perturbations (Nozaki et al. 2006). Likewise, opposing perturbations can be learned
during bimanual movements under different contexts such as the hands acting on a
single or two separate objects (Howard et al. 2008) or moving in the same or different
directions (Howard et al. 2010). In all these bimanual studies, modulation of the
motor representation associated with one limb appears to depend on the action (or
absence of action) performed by the opposite limb. This phenomenon requires active
movement because interference still occurs in the case where one arm is moved
passively (Howard et al. 2010). Importantly, in this case all other potential cues
except for active movement were the same. This suggests that in the current study, the
“contextual cue” must be the type of movement that is performed (rhythmic versus
discrete), rather than block identity.

Evidence that there is separate circuitry for rhythmic and discrete movements is
consistent with recent neuroimaging studies. For example, Schaal performed fMRI
experiments whilst subjects made discrete or rhythmic movements, which consisted
of single wrist joint flexion-extensions (Schaal et al. 2004). Their principle finding
was that rhythmic movements activated a small number of unilateral primary motor
areas, whereas discrete movement activated additional motor areas and showed strong
bilateral activity in both cerebrum and cerebellum. They concluded that this provides
evidence for separate control circuitry for discrete and rhythmic movements.

Several researchers have taken a more theoretical view when interpreting rhythmic
and discrete movements. For example, rhythmic movements have been modeled using
dynamical system theory, and such models can replicate many observed phenomena
in both unimanual and bimanual movements, such as the stability of preferred phases
and the transitions towards stable modes (Haken et al. 1985; Kay et al. 1987; Kelso
1984). A dynamical system analysis has also been extended to account for discrete
and rhythmic movements. Schoner proposed that the dynamical systems perspective
for understanding rhythmic movements could be generalized to account for discrete
movements (Schoner 1990). He showed that a dynamical system model can exhibit
discrete as well as continuous behaviors, using fixed point and limit cycle attractors,
respectively. Recently, discrete movements have been modeled within the framework
of optimal feedback control (Todorov and Jordan 2002). Although dynamical systems and optimal control have traditionally been considered separately, a framework has been proposed which unifies them allowing a single model to account for both rhythmic and discrete movements (Schaal et al. 2007).

Several other computational models have also been proposed to account for both discrete and rhythmic movements (Ronsse et al. 2009; Ronsse et al.). The implication is that these movement types constitute different movement primitives and in the case of combined movements, combinations of such primitives can occur. In most experimental studies, rhythmic and discrete arm movements are often studied in isolation, with little or no consideration to their interactions. Exceptions to this are found in studies involving the combination of discrete and rhythmic elements within movements (Staude et al. 2002; Sternad et al. 2002; Sternad et al. 2000). Such studies indicate that interaction occurs. For example, Sternad found that kinematic constraints for the coupling of discrete and rhythmic elements have a tendency to synchronize (Sternad et al. 2000). This was also the case for movements involving multi-joint coordination (Sternad and Dean 2003).

In conclusion, results from the current study show that associating opposing dynamic perturbations with rhythmic and discrete movement classes allows subjects to co-represent each perturbation and thereby learn dynamic perturbations which would otherwise interfere. Importantly, adaptation to the particular perturbation associated with each movement class was accompanied by large post-exposure after-effects which were specific for the perturbation, indicating predictive compensation. In contrast, post-exposure after-effects were not present in the static context
experiments, indicating that the reduction in error in this condition mainly arose due
to co-contraction. Overall, these results are consistent with the existence of control
mechanisms that are at least partially separate for rhythmic and discrete movement
classes.

Grants

We thank the Wellcome Trust and The European Project (SENSOPAC IST-2005-
028056, http://www.sensopac.org) for support.

Disclosures

The authors declare that they have no financial, personal, or professional interests
that could be construed to have influenced the paper.
**Figure Legends**

**Figure 1** Viscous skew fields and circular movements. **A** The viscous skew fields for perturbations P1. **B** The viscous skew fields for perturbations P2. **C** The elliptical deviation of a circular movement made in the viscous skew field P1 (in panel A). **D** The elliptical deviation of a circular movement made in the viscous skew field P2 (in panel B).

**Figure 2** Experiment 1: Static context – rhythmic movements. **A** Table showing the perturbation (P1 or P2), movement class (always rhythmic) and number of blocks for each perturbation. **B** Paths for a single representative subject. Plot colors follow those used for the perturbations in panel A and catch errors are shown in mauve. The upper row shows the paths during pre-exposure (Null-field, block 2), initial exposure in P1 (block 3) and final exposure in P1 (block 30). The lower row shows the paths during initial exposure in P2 (block 31), final exposure in P2 (block 58) and post-exposure (Null-field, block 59). **C** Signed mean error (solid line) and standard error (shading). Each point is the mean across subjects (n=6).

**Figure 3** Experiment 2: Static context – discrete movements. **A** Table showing the perturbation (P1 or P2), movement class (always discrete) and number of blocks for each perturbation. **B** Paths for a single representative subject. Plot colors follow those used for the perturbations in panel A and catch errors are shown in mauve. The upper row shows the paths during pre-exposure (Null-field, block 2), initial exposure in P1 (block 3) and final exposure in P1 (block 30). The lower row shows the paths during initial exposure in P2 (block 31), final exposure in P2 (block 58) and post-exposure
Signed mean error (solid line) and standard error (shading). Each point is the mean across subjects (n=6).

**Figure 4** Experiments 3-5: Switching perturbations – Paradigm. 

A Table showing perturbation (P1 or P2), movement class (always rhythmic) and block numbers in the

switching perturbation static rhythmic movement Experiment 3. B Table showing perturbation (P1 or P2), movement class (always discrete) and block numbers in the

switching perturbation static discrete movement Experiment 4. C Table showing perturbation (P1 or P2), movement class (rhythmic or discrete) and block numbers in the switching perturbation, switching movement class Experiment 5.

**Figure 5** Experiments 3-5: Switching perturbations – Results. 

A Paths for the static rhythmic movement Experiment 3 for a single representative subject showing odd (red) and even blocks (blue). The plot shows the paths during pre-exposure (blocks 1 & 2), initial exposure in P1 and P2 (blocks 3 & 4), final exposure in P1 and P2 (blocks 37 & 38) and post-exposure (block 39 & 40). B Paths for the static discrete movement Experiment 4, plotted as in panel A. C Paths for the switching rhythmic-discrete movement Experiment 5, plotted as in panel A. D Signed mean error (solid line) and standard error (shading) for Experiments 3-5. Each point is the mean across subjects (n=6). The static rhythmic movement from Experiment 3 is plotted in green. The switching rhythmic movement Experiment 5 is plotted in red. The static discrete movement Experiment 4 is plotted in blue. The switching discrete movement Experiment 5 is plotted in grey.
Figure 6 Experiment 6: Switching perturbation, static movement class – two-speed control. A Distributions of end-point velocity for the 1.1 Hz (first column) and 0.9 Hz (second column) rotation speed conditions across all trials and all subjects for the two-speed control Experiment 6. B Distributions of end-point position for the 1.1 Hz (first column) and 0.9 Hz (second column) rotation speed conditions across all trials and all subjects for the Experiment 6. C Mean speed and standard error for the duration of the trial, normalized for trial length, across all trials and all subjects for the 1.1 Hz (red) and 0.9 Hz (blue) conditions. D Signed mean error (solid line) and standard error (shading) for the two-speed control Experiment 6 (green) and for the static rhythmic movement Experiment 3 (red). Each point is the mean across all subjects (n=6).


Karniel A, and Mussa-Ivaldi FA. Does the motor control system use multiple models and context switching to cope with a variable environment? *Experimental brain research Experimentelle Hirnforschung* 143: 520-524, 2002.


<table>
<thead>
<tr>
<th>Perturbation</th>
<th>Null</th>
<th>Null</th>
<th>P1</th>
<th>P2</th>
<th>P1</th>
<th>P2</th>
<th>Null</th>
<th>Null</th>
</tr>
</thead>
<tbody>
<tr>
<td>Movement</td>
<td></td>
<td></td>
<td>Rhythmic</td>
<td>Rhythmic</td>
<td>Rhythmic</td>
<td>Rhythmic</td>
<td>Rhythmic</td>
<td>Rhythmic</td>
</tr>
<tr>
<td>Blocks</td>
<td>2</td>
<td></td>
<td>86</td>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Perturbation</th>
<th>Null</th>
<th>Null</th>
<th>P1</th>
<th>P2</th>
<th>P1</th>
<th>P2</th>
<th>Null</th>
<th>Null</th>
</tr>
</thead>
<tbody>
<tr>
<td>Movement</td>
<td></td>
<td></td>
<td>Discrete</td>
<td>Discrete</td>
<td>Discrete</td>
<td>Discrete</td>
<td>Discrete</td>
<td>Discrete</td>
</tr>
<tr>
<td>Blocks</td>
<td>2</td>
<td></td>
<td>86</td>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Perturbation</th>
<th>Null</th>
<th>Null</th>
<th>P1</th>
<th>P2</th>
<th>P1</th>
<th>P2</th>
<th>Null</th>
<th>Null</th>
</tr>
</thead>
<tbody>
<tr>
<td>Movement</td>
<td></td>
<td></td>
<td>Rhythmic</td>
<td>Discrete</td>
<td>Rhythmic</td>
<td>Discrete</td>
<td>Rhythmic</td>
<td>Discrete</td>
</tr>
<tr>
<td>Blocks</td>
<td>2</td>
<td></td>
<td>86</td>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Pre-exposure</td>
<td>Initial exposure</td>
<td>Final exposure</td>
<td>Post-exposure</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>----------------------</td>
<td>--------------</td>
<td>------------------</td>
<td>----------------</td>
<td>---------------</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>A</strong> Static rhythmic</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>B</strong> Static discrete</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>C</strong> Switching rhythmic/discrete</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

D: Pre-exposure, Exposure, Post-exposure

- Green - static rhythmic
- Red - switching rhythmic
- Blue - static discrete
- Grey - switching discrete

Signed error

Block pairs: 1, 20, 40
### A

**Velocity distributions**

<table>
<thead>
<tr>
<th>Rhythmic 1.1Hz</th>
<th>Rhythmic 0.9Hz</th>
</tr>
</thead>
<tbody>
<tr>
<td><img src="image1.png" alt="Image" /></td>
<td><img src="image2.png" alt="Image" /></td>
</tr>
</tbody>
</table>

### B

**Position distributions**

| ![Image](image3.png) | ![Image](image4.png) |

### C

**Mean speed (cm/s)**

- Red - 1.1Hz
- Blue - 0.9 Hz

![Graph](image5.png)

### D

**Signed error**

- Green - 2-speed control
- Red - original

![Graph](image6.png)