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Rhythmic movements are larger and faster but with the same frequency on removal of visual feedback

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Levy-Tzedek S, Ben Tov M, Karniel A. Rhythmic movements are larger and faster but with the same frequency on removal of visual feedback. *J Neurophysiol* 106: 2120–2126, 2011. First published August 3, 2011; doi:10.1152/jn.00266.2011.—The brain controls rhythmic movement through neural circuits combining visual information with proprioceptive information from the limbs. Although rhythmic movements are fundamental to everyday activities the specific details of the responsible control mechanisms remain elusive. We tested 39 young adults who performed flexion/extension movements of the forearm. We provided them with explicit knowledge of the amplitude and the speed of their movements, whereas frequency information was only implicitly available. In a series of 3 experiments, we demonstrate a tighter control of frequency compared with amplitude or speed. We found that in the absence of visual feedback, movements had larger amplitude and higher peak speed while maintaining the same frequency as when visual feedback was available; this was the case even when participants were aware of performing overly large and fast movements. Finally, when participants were asked to modulate continuously movement frequency, but not amplitude, we found the local coefficient of variability of movement frequency to be lower than that of amplitude. We suggest that a misperception of the generated amplitude in the absence of visual feedback, coupled with a highly accurate perception of generated frequency, leads to the performance of larger and faster movements with the same frequency when visual feedback is not available. Relatively low local coefficient of variability of frequency in a task that calls for continuous change in movement frequency suggests that we tend to operate at a constant frequency at the expense of variation in amplitude and peak speed.

motor control; frequency control; perception and action; timing; sensorimotor integration

FROM FISH TAIL BEATING to bird-wing flapping and man running, frequency, or the timing of movement, is an important parameter in movement control. However, is movement frequency controlled directly or simply the result of controlling other movement parameters? The ability to perceive accurately elapsed time and to generate accurately timed movements is fundamental in survival (Buhusi and Meck 2005). At the same time, the control of rhythmic movement, although phylogenetically old and preserved among species (Miall and Ivry 2004), has yet to be elucidated. Let us inspect, for example, three of the readily measurable movement parameters: frequency, amplitude, and speed. These parameters are not independent, as frequency is the quotient of speed and amplitude. It is therefore unlikely that all three of these parameters are set for a given movement but rather a subset of them. It is possible that our brain can directly control different movement parameters, and the choice of which is more tightly controlled depends on the nature of the specific movement, the instructions, the end effector, and the availability of the various feedback modalities (vision, proprioception, etc.). Here, we ask which of these three movement parameters is most tightly controlled when performing rhythmic forearm movements, with and without visual feedback (VF).

In control of rhythmic movement, neural circuitry input is combined with peripheral limb dynamics to produce movement. At the neuronal level, rhythmic activity is ubiquitous and plays an important part in various aspects of nervous system function, from sensory integration to central processing and motor control (Ayali and Lange 2010), with neuronal network activity covering frequencies from approximately 0.05 to 500 Hz (Buzsáki and Draguhn 2004). Models were developed that suggest that the output of a central pattern generator [hypothesized to be combined with cortical input in the control of rhythmic arm and leg movements (Zehr et al. 2004)] can be entrained to match the resonant frequency of the moving limb (Hatsopoulos 1996; Verdaasdonk et al. 2006).

An extensive body of research on locomotion and on rhythmic movements of the upper limbs suggests that we tend to move at, or close to, the resonant frequency of the limb, as determined by its mechanical properties (e.g., Goodman et al. 2000; Kubo et al. 2004; White et al. 2008). The resonant frequency, in turn, may be tuned by changing the stiffness of the limb to match task requirements (Kay et al. 1987). The concept of a "preferred amplitude" has also been put forth, and it has been suggested that there is a tendency to move the limb at a preferred amplitude in the absence of an external pacemaker (Yu et al. 2003).

We ask whether the brain is able to control frequency, amplitude, and peak speed equally well. If the answer is yes, then the "best controlled parameter" would be a different parameter for different tasks, depending on the task instructions and on the nature of the available feedback. Otherwise, if we consistently control one parameter better than the others, it should be the best controlled parameter regardless of the task instructions and the available feedback.

Here, we demonstrate that despite being asked explicitly to control movement amplitude and speed, participants maintain low variability in implicitly specified frequency. When rhythmic forearm movements were performed in the absence of VF, the movements were consistently larger and faster than required while maintaining movement frequency. To investigate the basis of this behavior, we examined the effect of awareness of this increase in amplitude and speed on performance in a

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second experiment. We found the same result even when participants were aware of the discrepancy. This behavior is likely the result of a mismatch between the perception of and the actually generated amplitude and speed, contrasting with a highly accurate perception of the generated frequency. To examine further the possibility that frequency is better controlled when performing rhythmic movements, we tested, in a third experiment, performance on a task where frequency and speed, but not amplitude, must be changed during a trial. Here, too, we found evidence for frequency being more tightly controlled compared with amplitude and speed.

MATERIALS AND METHODS

Experimental protocol. Participants (n = 39, age: 24.9 ± 2.8 yr; mean ± SD) were asked to perform one-dimensional horizontal flexion/extension movements with their forearm about their elbow (Fig. 1*A*). The forearm was placed in a wrist brace, strapped to an armrest, and mounted on a table in front of the seated participant. The forearm support was connected to the shaft of a rotary incremental encoder with a position resolution of 0.002° per count. Data were recorded at 200 Hz. Both the angular position and the angular velocity of the forearm were displayed in real-time on a computer screen situated in front of the participants. A large, opaque cover was placed parallel to the table and above the apparatus, such that during the experiment, the participant's forearm was not visible. Participants were presented with a phase-plane display: the horizontal axis displayed angular position, and the vertical axis displayed angular velocity (see Fig. 1*B*). Participants were asked to perform these flexion/extension movements with their forearm such that the trace of their movement remains within a specified closed shape, delimited by two ellipses displayed on the screen, forming a doughnut shape (Levy-Tzedek et al. 2010, 2011a,b). Each ellipse corresponds to a sinusoidal motion about the elbow, with the nonzero width of the doughnut shape allowing for a range of amplitudes, speeds, and therefore frequencies (Doeringer and Hogan 1998). No explicit timing cues were given to participants. Timing on this task was emergent, as the frequency of the movement was determined by the combination of the amplitude and the speed of the movement (instructed by the phase-plane display). An explanation of the phase-plane display was given (horizontal axis corresponds to amplitude, vertical axis corresponds to velocity), and participants were free to practice movement with phase-plane feedback until they felt comfortable with the task. In trial segments where VF was available, participants could see the doughnut-shaped target region as well as a trace corresponding to their own forearm motion. When VF was not available, the doughnut-shaped target region was still displayed on the screen, but the participants did not see a trace corresponding to his or her own forearm motion. The participant's forearm was occluded from view throughout the experiment (see Fig. 1*A*). It is important to stress that when VF was available, participants had direct feedback on movement amplitude and speed only. No direct feedback was given regarding movement frequency. The participant population was divided into three groups, corresponding to three experimental protocols. At the beginning of each protocol, the preferred amplitude and frequency of each participant's forearm movements were recorded by asking the participants to rest their forearms in the armrest and perform rhythmic flexion/extension movements. Instructions were kept to a minimum at this stage so as not to bias movement parameters such as speed or amplitude. No VF was given during these recordings. Four recordings of the natural movement were performed in sequence, each lasting 20 s. The first two recordings were discarded, and the average of the last two recordings was used in determining the preferred amplitude and frequency values. All participants were naïve to the task.

In *experiment 1* (n = 13, 7 males, 6 females), the starting requirement in each of 4 trials was to move at 100 or 165% of the preferred values. Two consecutive trials were performed with an initial requirement to move at 100% of the preferred values, and two consecutive ones were performed with an initial requirement to move at 165% of the preferred values. Roughly half of the participants were first required to move at 100% of the preferred values, with the order reversed for the other part of the participant group. VF was alternately available during the movement (see Fig. 2, *top*), and whenever it was not available, the momentary amplitude and frequency of the movement were calculated, and became the required values for the subsequent trial segment, with VF. That is, the amplitude and the frequency of the participants' actual movement during the blind segments replaced the initial requirements for the following segments with VF. For example, if the initial requirement were to move at 100% of the

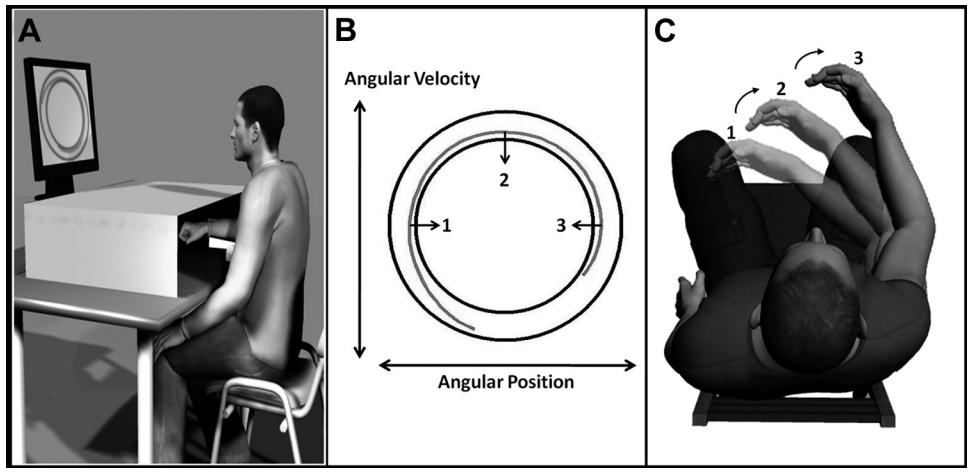

Fig. 1. *A*: the experimental setup illustrated. The participant's forearm is placed on a hinged armrest, allowing 1-dimensional horizontal movements. The forearm is covered, and visual feedback (VF) of the movement is given on the screen in the form of a phase-plane display: the black ellipses denote the limits of the required ranges of amplitude and speed, and the gray line represents the trace of the participant's movement on the phase plane (during the experiment the movement trace was shown in red). *B*: the phase-plane display, used in all 3 experiments, showing angular velocity vs. angular position (here, with axis labels). The area between the 2 black ellipses is the region within which participants are required to maintain the trace of their movement. The gray trace corresponds to the participant's movement in the phase plane (in the VF trials). The numbers 1 and 3 denote the 2 extreme positions of the participant's movement (flexion and extension, respectively), and the number 2 denotes the location where the movement speed peaks. *C*: a top view of the participant's forearm at 3 points along the movement trajectory (the numbers 1–3 correspond to the phase-plane locations marked in *B*). For the sake of clarity, the experimental apparatus is not depicted in this panel.

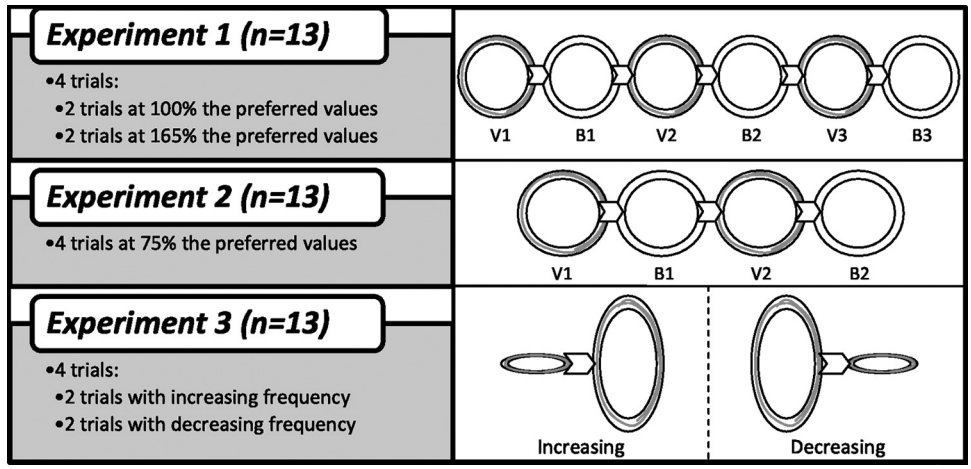

Fig. 2. Schematics of the 3 experimental protocols. On the left-hand side is a description of the protocol, and on the right-hand side, the display on the screen. The black ellipses denote the required ranges of amplitude and speed (continuously presented on the screen), and a gray line represents the trace of a participant's movement shown on the phase plane [when VF is available (V)]; empty "doughnuts" demonstrate that VF in the form of a movement trace was not provided ["blind" segments (B); numbers denote segment number]. Arrows denote a change in VF within a trial.

preferred values of amplitude and frequency, and during the first blind segment (B1; see Fig. 2) the participant moved at 120% of the required (preferred) values, then at the subsequent VF segment (V2), the participant would be required to move at 120% of the preferred values. Each trial segment with VF lasted 10 s, and each blind segment (no VF) lasted 15 s. A total of 312 trial segments were analyzed (13 subjects × 4 trials × 2 feedback conditions × 3 repetitions of each feedback condition per trial).

In *experiment 2* (n = 13, 6 males, 7 females), the protocol was similar to that of *experiment 1*, but in this nonadaptive protocol the required amplitude and frequency values remained fixed and did not change during the no-vision segments. Consequently, if participants made larger, faster movements in this protocol, they would become explicitly aware of this when VF became available after a blind segment. The participants were required to perform movements at 75% of the preferred values in each of 4 trials, where this requirement did not adaptively change during the trial (as in *experiment 1*) but remained constant (see Fig. 2, *middle*). Each trial segment with VF lasted 10 s, and each blind segment lasted 20 s. A total of 208 trial segments were analyzed (13 subjects × 4 trials × 2 feedback conditions × 2 repetitions of each feedback condition per trial).

In *experiment 3* (n = 13, 6 males, 7 females), in each of 4 trials, required amplitude was confined within a fixed range, whereas the required speed, and hence the required frequency, varied continuously. Target frequency was gradually increasing or decreasing between 0.2 and 3.1 Hz (see Fig. 2, *bottom*), and participants were required to modulate their movements accordingly to maintain the trace of their movements within the enclosed area on the phase plane. Each trial lasted 64.5 s. Roughly half of the participants performed 2 consecutive increasing-frequency trials followed by 2 consecutive decreasing-frequency trials, with the order reversed for the other part of the participant group.

In all trials of all 3 experiments, 1 extra second of movement was added at the beginning of the trial, and 1 at the end. These were not recorded, to avoid edge effects.

The local Helsinki Committee approved the experimental protocol. All participants gave their written informed consent to participate.

Expected value for frequency coefficient of variability. It is expected that if participants control amplitude and speed, as instructed to do, these parameters will have lower values of coefficient of variability (CV) compared with the movement frequency, which is expected to be emergent rather than directly controlled. Under the assumptions of two independent, uncorrelated random variables (a and s; Silverman et al. 2004) that form the relationship $f = s/a$, the approximation of the ratio can be achieved by using a Taylor series expansion of the variance. Therefore, the frequency CV would be predicted to obey the following relationship (Holmes and Buhr 2007):

$$CV_f \cong \frac{\sqrt{CV_s^2 + CV_a^2 + 3CV_a^2CV_s^2 + 8CV_a^4}}{1 + CV_a^2}$$

where CV_f, CV_s, and CV_a are the CV of frequency, peak speed, and amplitude, respectively.

For calculation of "local" CV, the data from each 64.5-s trial in *experiment 3* were parsed into 31 bins, each averaging ~2 s in duration. Within each bin, the local CV values of each parameter (frequency, peak speed, and amplitude) were calculated as the standard deviation of the data in the bin divided by the mean of the data in the bin. CV values were then averaged across the entire trial. A total of 1,612 bins were analyzed (13 subjects × 4 trials × 31 bins per trial).

Statistical analysis. Repeated-measures ANOVA was applied to the data as follows:

In *experiment 1*, a 2 (feedback condition: with/without VF) × 2 (initial condition: 100/165% of preferred values) × 13 (participants) ANOVA was applied to the data.

In *experiment 2*, a 2 (feedback condition: with/without VF) × 13 (participants) ANOVA was applied to the data.

In *experiment 3*, a 4 (metric: amplitude/peak speed/actual frequency/expected frequency) × 13 (participants) ANOVA was applied to the data.

P values <0.05 were considered to indicate a significant difference.

RESULTS

Preferred frequency and amplitude values from the three experiments are shown in Fig. 3. Average preferred frequency was 0.69 ± 0.03 Hz (mean ± SE, range: 0.28–1.31 Hz), and average preferred amplitude was 63.1 ± 3.4 (range: 27.1–106.0°).

In all three experiments, when VF was available, participants' accuracy levels, that is, the percentage of the time spent inside the target closed shape on the phase plane, were comparable with those reported in Levy-Tzedek et al. (2010).

Experiment 1: larger, faster movements in the absence of VF. There was a consistent increase in the area taken up on the phase plane by the movements of the participants (capturing the increase in amplitude and speed; see Fig. 4*A*; note that we discuss the findings in terms of the phase-plane area, which captures the changes in both amplitude and speed; however, the reported trends apply to amplitude and peak speed when analyzed separately as well) in the blind segments compared with the preceding vision segments (positive values in Fig. 4*B*; phase-plane area and frequency values from each segment were normalized by the corresponding values obtained from the preferred-movement recordings; the differences, in per-

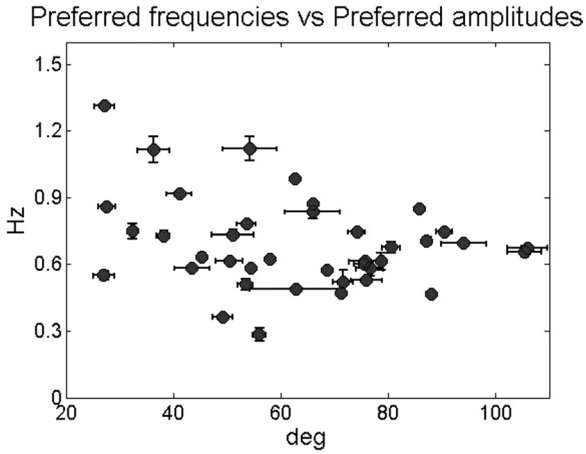

Fig. 3. Preferred values of frequency (in hertz) vs. preferred values of amplitude (peak-to-peak, in degrees) for all 39 participants. Error bars represent standard error.

centages, between consecutive segments are reported in the figure. The phase-plane area during the blind segments was significantly larger than during the vision segments [$P = 0.0082$, with blind segments 8.7 ± 3.7% (mean ± SD) larger than preceding vision segments and vision segments 16.6 ± 0.1% smaller than preceding blind segments; see Fig. 4*B*], whereas frequency remained approximately constant across segments (blind segments 1.6 ± 0.6% larger than preceding vision segments and vision segments 0.1 ± 2.2% larger than preceding blind segments; not significant). Thus, despite the adaptive protocol, which offered participants the possibility to move at smaller amplitudes and slower speeds by slowing down and making smaller movements during the blind segments, and even in trials where the initial conditions called for movement at 165% of the preferred values, participants consistently increased the phase-plane area taken up by their movements in the absence of VF.

Experiment 2: larger, faster movements in the absence of VF despite awareness. Although 11 of the 13 participants reported that they were aware that their movements were larger and/or faster during the blind segments, there was still a significant increase in phase-plane area in subsequent blind segments [$P < 0.0001$, with blind segments 133.0 ± 4.2% and vision segments 102.4 ± 3.3% of the 1st (vision) trial segment]; no significant difference was found in frequency ($P > 0.5$, 100.4 ± 0.6 and 99.4 ± 0.8%, respectively; see Fig. 4*C*). We stress that the participants were instructed to perform movements for which the trace on the phase plane remained within a predefined area on the phase plane, and there was no explicit mention of movement frequency (Levy-Tzedek et al. 2010, 2011a,b); despite this, during the blind segments, they apparently ignored the instructions by increasing movement amplitude and peak speed while maintaining a relatively constant movement frequency.

The increase in amplitude of the rhythmic movements occurred away from the participants' preferred amplitude toward larger values and despite awareness of this behavior and declared efforts to attenuate it.

Experiment 3: lower CV in frequency compared with amplitude despite opposing task requirements. The CV of frequency of the performed movements, calculated locally, was significantly lower than those of amplitude and peak speed (Allison 1978; Houle et al. 1996; Kay et al. 1987, Table 1). It was also significantly lower than the expected value if frequency were simply the ratio of speed to amplitude (see Fig. 5), consistent with an interpretation that we are better at controlling movement frequency and refuting the null hypothesis asserting that speed and amplitude, but not frequency, are being controlled in this task. The expected value is calculated according to the formula for the CV of a ratio of two variables

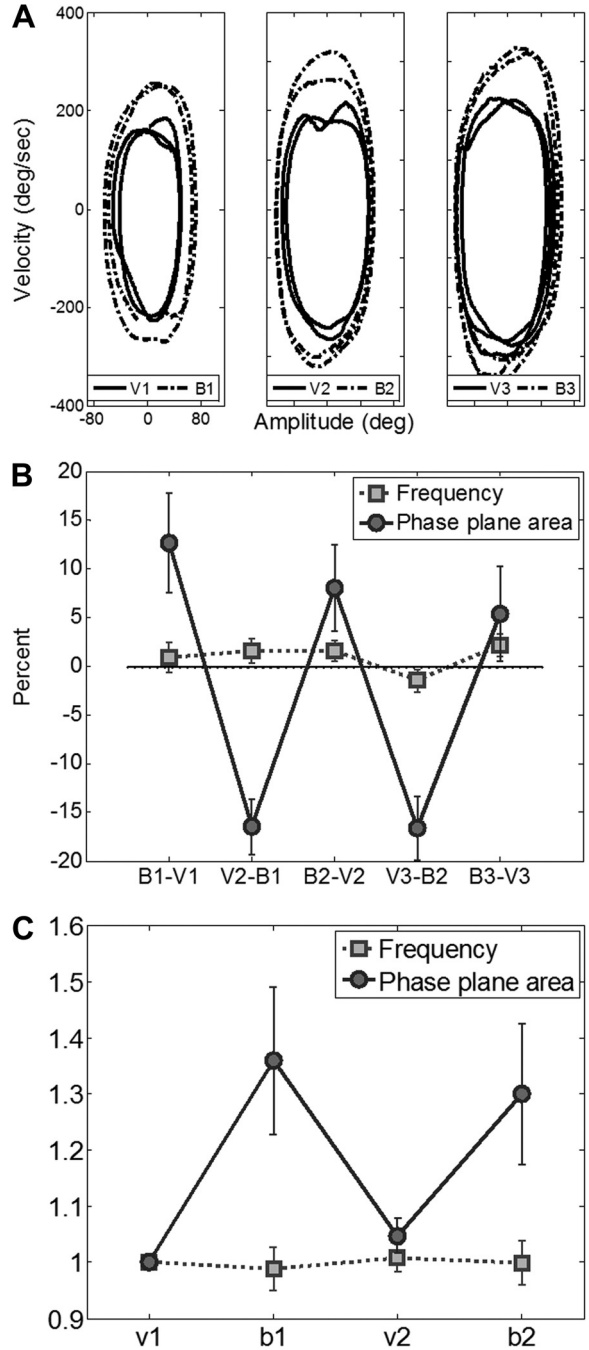

Fig. 4. *A*: phase-plane plot showing a participant's movement trace during the 6 trial segments (numbers denote segment number) in *experiment 1*. *B*: the differences between consecutive trial segments in phase-plane area and frequency normalized by each participant's preferred values (shown as percentage); horizontal black bar denotes 0 difference (*experiment 1*). *C*: phase-plane area and frequency values in the 4 trial segments in *experiment 2*, normalized by the 1st segment of the trial (V1). Error bars represent standard error.

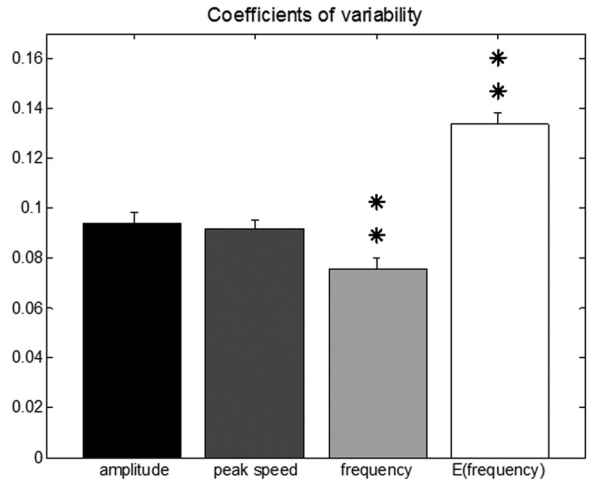

Fig. 5. The coefficients of variability (CV) of amplitude, peak speed, frequency, and expected (E) frequency (if amplitude and speed, but not frequency, are directly controlled; see MATERIALS AND METHODS) in *experiment 3*. Two asterisks above a column denote that its value is significantly different from all other columns ($P < 0.0001$).

(Holmes and Buhr 2007). It should be noted that our result is robust and insensitive to the approximation used to calculate the CV of the ratio. Although the above cited formula is derived from third- and fifth-order Taylor series expansions, a significant difference was also found when using first- and third-order Taylor series expansions to calculate the expected CV.

It should be stressed that participants were given explicit feedback on the position and velocity of their one-dimensional horizontal forearm flexion/extension movements. Frequency information was thus only indirectly available.

DISCUSSION

We have shown that participants make larger and faster movements in the absence of VF while maintaining the same movement frequency when performing rhythmic movements of the forearm. In fact, participants were able to synchronize to an implicitly specified tempo, and code it internally, such that even the implicit specification was not necessary (during the blind segments) for accurate production of the correct tempo. The increase in amplitude of the rhythmic movements occurred even when initial values were greater than the participants' preferred amplitude and despite awareness of this increase and declared efforts to attenuate it. It might be argued that there is no preferred amplitude at all, although the mostly short horizontal error bars in Fig. 3 suggest otherwise. However, if there is a preferred amplitude, then surely we did not miss it: we tested participants who made movements for which the amplitude ranged from 75 to 165% of the preferred amplitude (which in some cases was near the physical limit of movement) and still observed an increase in size on removal of VF. We conclude that there is a uniform tendency to perform larger, faster movements, which is not dependent on the preferred amplitude value. These results seem to suggest that the increase is not the result of gravitation toward a preferred amplitude but is likely the result of misestimation of the generated amplitude, possibly perceived as smaller than its actual value (Soechting and Flanders 1989; c.f. Wolpert et al. 1995), possibly reflecting a degraded performance of proprioception compared with vision (Ernst and Banks 2002; for a parallel finding in generation of force, see Shergill et al. 2003). At the same time, the low variability in generation of movement frequency demonstrates that frequency control is accurate regardless of the presence of VF, implying frequency estimation is highly accurate regardless of the availability of VF. It is important to note that the consistent frequency output is not simply biomechanical (as might be the case when moving at the resonant frequency), since this behavior is maintained over a wide range of velocities and amplitudes. In fact, our results show that even when participants were asked to modulate movement frequency, but not amplitude, the CV of frequency was significantly lower than that of amplitude (and also significantly lower than the CV of peak speed, which was also modulated continuously).

It is possible that the more consistent frequency output, compared with the amplitude and speed output, is not the result of a hierarchical control mechanism in which frequency is preferentially controlled but rather emerges, for example, as a result of the quality of incoming sensory information regarding each of these parameters. That is, assuming that the perception of the generated movement time is superior to the perception of the generated amplitude and speed, as we suggest above, this difference in perceptual acuity may be reflected in the output of the motor command, which will be more variable in amplitude and speed than in frequency.

An alternative explanation for the increase in amplitude and speed in the absence of VF is that the mechanism controlling the rhythmic movement can better stabilize its frequency output when it receives stronger proprioceptive feedback (for related evidence in locust flight, see Ausborn et al. 2007). Stronger proprioceptive feedback, in turn, may be provided by larger, faster movements (Goble et al. 2006).

It is important to note that the finding we report, of an amplitude increase on removal of VF, is not unique to the particular experimental setup used in the three current experiments. Yu et al. (2003) reported a similar finding: in their task, participants were asked to swing a pendulum with their wrist at frequencies that were either higher or lower than their preferred frequency. Target amplitude was constant and was determined based on the average of preferred amplitudes in a pilot study. A continuation paradigm was used: following a synchronization period with VF, feedback was withdrawn, and participants were asked to continue the movement. The authors found that participants consistently performed larger-amplitude movements during the continuation phase. They concluded that the study participants' preferred amplitude must have been larger than the target amplitude and that this upward drift in amplitude is the result of a drift toward the preferred value. However, this assertion was not anchored in the experimental evidence provided in that study. We suggest an alternative interpretation of their findings, given the results we report here, whereby the consistent increase in amplitude of rhythmic movements in the absence of an external pacemaker is the result of underestimation of the generated amplitude.

How may we account for the difference in the CV values of the three movement parameters we report here? The "minimal intervention" principle, introduced by Todorov (2004), states that variability is allowed in task-irrelevant dimensions (see also the "uncontrolled manifold hypothesis," Scholz and Schöner 1999). Deviations from the average trajectory are

corrected only when they interfere with task performance. The experimental data presented here can be interpreted, using the minimal-intervention principle, as indicating that we assign the highest importance to the movement frequency when performing rhythmic movements even when not explicitly instructed to do so and regardless of availability of VF. Accordingly, one possible interpretation of the presented data is that the controller attempts to minimize variation in frequency rather than in amplitude and peak speed.

Any attempt to characterize the control mechanism that produces the speed, amplitude, and frequency of the movement must take into account that the three parameters cannot be controlled in a manner completely independent of each other, as stated in the Introduction. Indeed, previous studies have reported a link between movement amplitude and frequency (e.g., Kay et al. 1987; Peper and Beek 1998). However, although under certain conditions a covariation of these two parameters is observed, there is ample evidence for the two being separately controlled (Schöner 2002). Kay et al. (1987), analyzing frequency-amplitude relations within what they defined as the stable region of behavior (1–2 Hz, comparable with the frequencies reported in the current study), found no concurrent change in amplitude with frequency in either single-handed or bimanual movements. Note that these authors recorded shorter durations of movement at high movement frequencies "to minimize fatigue." This alludes to the importance of energy expenditure in movement control and may underlie the suggested decrease in amplitude with increasing frequency at higher movement frequencies. Indeed, this effect appears to be most prominent at the extremes of movement. It is also important to note Table 1 in that study where the movement frequency CV is overall lower than those of amplitude and peak speed, consistent with the results of the current study; Hollerbach (1981) found that, when producing rhythmic handwriting movements, handwriting frequency is independent of writing size; and Peper and Beek (1998) demonstrated that frequency-induced transitions in rhythmic movements were not mediated by a change in amplitude, but rather they occurred whether amplitude increased or decreased. These studies, together with the current one, support a separate control of frequency and amplitude.

The reported observations are consistent with an interpretation that frequency is directly controlled when performing rhythmic movements. This interpretation is supported by evidence from neuronal recordings suggesting that neuronal ensembles (Sumbre et al. 2008) and even single neurons (Komura et al. 2001) can code timing information and may act as adjustable "metronomes," which might serve to generate accurate timing on a task. In fact, it has been hypothesized that our brain is host to a dedicated system for timing (Ivry and Schlerf 2008; Ivry and Spencer 2004). Patient studies, including individuals with cerebellar damage, with supplementary motor area (SMA) lesions and ones with Parkinson's disease suggest that timing may be encoded in the cerebellum, the basal ganglia, and/or the SMA (Freeman et al. 1993; Grondin 2010; Ivry and Keele 1989; Rao et al. 1997). It is suggested that the performance of precisely timed movements is dependent on three interrelated neural circuits, the medial premotor circuitry, the right superior temporal gyrus, and the right inferior frontal gyrus, and the dorsal dentate nucleus and the sensorimotor cortex, each serving a unique function (Rao et al. 1997). The specific contribution of the cerebellum to movement timing is a topic of debate in the literature. Some researchers suggest that its role is to perceive the duration of events (Ivry and Keele 1989; Mangels et al. 1998), whereas other researchers suggest that the timing variability that is observed in cerebellar patients is the result of deficits in sensorimotor prediction (Bo et al. 2008; Diedrichsen et al. 2007). Interestingly, control of movement timing and amplitude may not be done by completely separate circuits, but the two might be linked within the cerebellum, as suggested by the association between cerebellar dysmetria and impaired rhythm generation (Manto 2009).

The results we report here, although informing us about brain mechanisms as detailed above, also have a potential impact on rehabilitation. For example, the increase in movement speed on removal of VF, shown to occur in patients with Parkinson's disease who suffer from bradykinesia (slowness of movement; Levy-Tzedek et al. 2011b), can be harnessed to develop novel physical therapy approaches for these patients. For a successful design of intelligent interfaces with humans (e.g., Karniel et al. 2010), we must first understand which movement parameters are more tightly controlled. Here, we demonstrated a preference for a tighter control of movement frequency over amplitude and speed when performing rhythmic movements of the forearm.

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GRANTS

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

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