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# Reaction–anticipation transitions in human perception-action patterns

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## Abstract

We investigated the hypothesis that reaction and anticipation in human perceptual-motor performance are two coordinative modes of a single pattern-forming dynamical system, rather than separate behaviors. Subjects coordinated the onset of finger flexions with visual metronome flashes in each of three patterns: *reactive*, *synchronized*, or *syncopated*. The stimulus frequency was progressively increased (0.125–1.375 Hz) or decreased (1.375–0.125 Hz) in small steps (0.125 Hz) every 10 cycles. We observed qualitative transitions in both the time interval between stimulus and corresponding action ( $\Delta t$ ) and their relative phase ( $\phi$ ) at critical values of the stimulus frequency, corresponding to changes from ‘reactive-to-anticipatory’ and ‘anticipatory-to-reactive’ performance. Such transitions provide evidence of a single, multifunctional system, which can be adequately described by the dynamics of collective variables characterizing the respective perception-action patterns.

*PsycINFO classification:* 2300; 2500

*Keywords:* Coordination dynamics; Reaction; Synchronization; Switching

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## 1. Introduction

Somehow, organisms can routinely coordinate their actions both with unexpected and expected external events, reacting to them or anticipating them, respectively. Both of these abilities require interaction of organism and environ-

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ment, and together are vital for survival (for example, driving vehicles; crossing streets; catching objects (Savelsbergh et al., 1992); folding of wings in plummeting gannets (Lee and Reddish, 1981); optimal foraging (Krebs et al., 1974)). How are reaction and anticipation accomplished? Are they independent or related processes? What are the limits of reaction and anticipation? So far, these questions remain unanswered. This is surprising when one considers the huge amount of research into the production and organization of temporal patterns in humans (e.g., Bartlett and Bartlett, 1959; Deecke et al., 1976; Dunlap, 1910; Hary and Moore, 1985, 1987; Libet et al., 1982, 1983; Jeannerod, 1984; Kristofferson, 1984; Michon, 1967; Pöppel et al., 1990; Rosenbaum and Patashnik, 1980; Wing, 1980; Woodrow, 1932) and animals (e.g., Sismondo, 1990; Gibbon and Church, 1981; Mandell and Atak, 1982). The literature is much more extensive for reaction than anticipation; only a small amount of research exists regarding their possible interaction (e.g., Hah and Jagacinski, 1994; Magdalenio et al., 1970; Mates et al., 1994; Fender, 1964).

Robert Rosen (1985) stated that the dearth of systematic contemplation and study of anticipatory systems is not simply an oversight, but rather a consequence of the preoccupation of the scientific community with 'normal' causality: in any law governing a natural system, it is forbidden to allow present change of state to depend upon future states. In an attempt to resolve this issue, Rosen (1985) speculated that if anticipatory systems create predictive inner models of their environment, and utilize predictions of these inner models to modify their present behavior, causality need not be violated. Rosen's predictive inner model explanation of anticipatory behavior raises some important questions. How are such models created? How and where are they stored and then accessed to produce successful anticipatory behavior? Furthermore, inner models are potentially homuncular in nature, raising the spectre of infinite regress (i.e., inner models requiring inner models *ad infinitum* – see discussion in Rosen, 1985). But, according to Rosen, infinite regress might be overcome if the inner models were required to be grounded within an environmental context (Rosen, 1992, personal communication). In a sense, contextual coupling with the environment would provide the system with an opportunity to 'break the chain' of regression (e.g., Gibson, 1979; Turvey et al., 1990; Turvey and Kugler, 1984; Warren, 1984). However, such mandatory environmental coupling necessarily results in a switch of emphasis from inner models to *modelling relations* (Rosen, 1985), a movement from *within* to *between*. We suggest that the modelling relation may be understood as a self-organized pattern formation process between organismic and environmental variables, and as such, does not require homunculi (Kelso et al., 1990; Kelso, 1991).

It is clear that both reactive and anticipatory coordinative patterns between organism and environment are essential for survival. Curiously, though studies of reactive and anticipatory behavior are seemingly straightforward, they are surprisingly difficult to interpret and understand. This may in part be due to an unreasonable segregation of these coordinative patterns into separate behaviors. In fact, we hypothesize that reaction and anticipation are two overlapping modes of a single, multifunctional coordinative system. In support, there is recent evidence demonstrating that brain activity specific to both reactive and anticipatory behavioral changes is spatiotemporally coherent over the entire cerebral cortex (Kelso et al., 1992; Wallenstein et al., 1995).

We propose here that an understanding of reaction and anticipation may be found by a study of their interaction. Such studies should provide crucial information for future design of all types of cognitive experiments involving repetitive stimuli. In the ideal, no reliance upon ad hoc notions about causality nor homuncular theoretical constructs should be necessary.

We pursued this aim by experimentally testing predictions of a well established theoretical framework based on the concepts of synergetics (Haken, 1983). Especially in situations where behavior changes qualitatively, synergetic systems are able to self-organize different coordinative patterns (or behavioral attractors) as a function of nonspecific control parameters (e.g., Haken et al., 1985; Kelso, 1984, 1995; Schöner and Kelso, 1988). In a large number of different systems, at critical values of experimentally tunable control parameters, transitions between coordinative patterns are observed (Kelso et al., 1988; Kelso, 1990). Such transitions involve a characteristic loss of stability of the current coordinative pattern (e.g., Kelso, 1984; Kelso and Scholz, 1985). Importantly, previous studies have demonstrated that human perception-action may be understood in terms of synergetic concepts and the language of dynamical systems (e.g., Kelso et al., 1990; Wimmers et al., 1992; Zanone and Kelso, 1992). In this study, we consider the possibility that reaction and anticipation are patterned behavioral states or attractors of a single, multifunctional perception-action system. If so, it should be possible to demonstrate that both reactive and anticipatory behavior are stable, identifiable behavioral modes at some values of a control parameter, yet unstable at others. Moreover, at critical values of the control parameter, transitions may be observed from one functional mode to the other. Of course, this strategy assumes the possibility of identifying relevant collective variables characterizing the patterned interaction between perceptual and motor components, as well as appropriate control parameters.

The task employed here extended a paradigm introduced by Kelso et al. (1990). Subjects were required to coordinate flexion-onsets of their preferred index finger 1:1 with serial visual metronome flashes in each of three patterns: (1) *reactive* (i.e., after perceiving each metronome flash); (2) *synchronized* (i.e., with metronome flashes); or (3) *syncopated* (i.e., halfway between metronome flashes). The metronome frequency was employed as a tunable control parameter, and progressively increased or decreased in small steps. The metronome frequency range was chosen to include frequencies that previous experiments had shown to be difficult for subjects to form anticipatory patterns (i.e., lower than 0.5 Hz (Dunlap, 1910; Bartlett and Bartlett, 1959; Magdaleno et al., 1970; Pöppel et al., 1990)) as well as frequencies at which they find it easy to do so (e.g., between 0.5 and 2 Hz). In the latter frequency range, the ability to generate simple serial reactions may be impeded by the tendency to anticipate oncoming stimuli.

The goal of this study was to test the hypothesis that adjusting an appropriate experimental control parameter, in this case, the stimulus frequency, results in characteristic transitions from reactive to anticipatory patterns and vice versa. Although recent (e.g., Mates et al., 1994) and past research has studied the synchronization process in detail, such research has neither varied a parameter over a sufficiently broad range of values, nor established initial conditions (e.g., starting the subject in a reactive mode) that could be transformed by changes in such parameters. As a consequence, the possibility of dynamics, e.g., (multi)stability, instability, etc., has not been adequately explored. The presence of dynamical effects would certainly inform current ideas about reaction, anticipation and their relationship.

## 2. Methods

### 2.1. Subjects

Ten normal adults, five male and five female, volunteered for this experiment and were not paid for their participation. Eight of the ten subjects were naive to the purpose of the experiment; two were not. All subjects were right-handed.

### 2.2. Apparatus

Flexion–extension movements of the subject's preferred index finger were recorded using an apparatus similar to the one described by Kelso and Holt

(1980). The apparatus consisted of an axle connected to a metal sleeve into which the subject's finger was inserted. A linear potentiometer connected to the axis of rotation allowed for the direct transduction of the continuous angular position of the finger about the metacarpophalangeal joint as the finger cycled in the transverse plane. The stimulus, a periodic visual signal of adjustable frequency, was generated by a PC-driven metronome. This signal was output and then conditioned to produce a train of 40 ms square wave pulses. These pulses were in turn used to drive an LED, producing a series of brief light flashes. Both the square wave signal of the metronome and the finger position signal were digitized at 200 Hz, stored in a micro-VAX computer, and saved for later analyses.

### 2.3. Procedure

Subjects were instructed to coordinate flexion-onsets of their preferred index finger with the serial metronome flashes 1:1 under each of three different conditions: *reactive*, so that each flexion-onset occurred as soon as possible after each metronome flash was perceived; *synchronized*, so that each flexion-onset occurred simultaneously with metronome pulses; or *syncopated*, so that each flexion-onset occurred exactly halfway between metronome pulses (Fig. 1). Subjects performed all conditions, administered on three separate testing sessions. The tasks were performed with two temporal progressions: an ascending metronome series in which the frequency of the metronome was increased from 0.125 Hz to 1.375 Hz in steps of 0.125 Hz, or a descending metronome series in which the metronome frequency was decreased from 1.375 Hz to 0.125 Hz in steps of 0.125 Hz. In all cases, the metronome produced 10 cycles at each frequency. Each condition was tested using both temporal progressions. Each subject performed a block of five trials for each experimental condition; the order of experimental conditions presented to each subject was randomized.

Subjects were seated comfortably in a chair in front of the apparatus. The height of the chair was adjusted to permit the forearm to rest horizontally on a padded support at the front of the apparatus. A soft adjustable plastic splint secured around the subject's forearm provided additional support and also served to restrain any unwanted movements of the wrist and fingers. A plastic shim was fit to the subject's index finger that was then inserted into the metal sleeve of the apparatus up to the first interphalangeal joint. Correctly positioned, the sleeve prevented movements of the two distal finger joints. The position of the hand was then adjusted and fixed so that the center of rotation of the metacarpophalangeal joint was colinear with the axis of rotation of the apparatus.

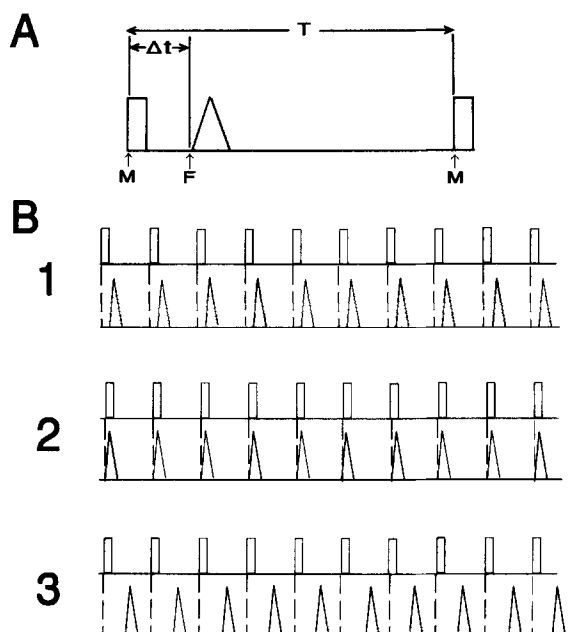


Fig. 1. (A) Measurement of putative collective variables for timing behavior:  $M$  – stimulus onset;  $F$  – flexion onset; metronome flash–response interval,  $\Delta t = F(n) - M(n)$ , is the difference in real time between stimulus flash and corresponding onset of flexion (note: if response precedes stimulus,  $\Delta t$  is a negative value). Relative phase,  $\phi = \Delta t / T \times 2\pi$ . (B) Idealized examples of coordinative modes through a single 10 cycle frequency plateau. (1) Reactive condition. Subjects were requested to provide flexions as quickly as possible after perceiving each stimulus. (2) Synchronized condition. Subjects were requested to synchronize flexion onset with the metronome onset. In the picture we see idealized performance, each response beginning exactly at the moment of stimulus onset. (3) Syncopated condition. Subjects were requested to begin movement exactly midway between two stimulus pulses.

After positioning the subject in the apparatus, instructions were issued. Each subject was given a description of the current experimental condition and instructed to cycle his/her finger once for each flash of the metronome maintaining the required coordination pattern as well as possible. Subjects were further instructed that should they feel the coordinative pattern begin to change they should not try to resist; it was emphasized that the primary task was to follow the metronome, maintaining one finger flexion for each metronome flash. This instructional set is equivalent to the ‘do not intervene’ instruction in single limb and bimanual motor control studies. Reactive, synchronized and syncopated conditions were demonstrated to each subject in order to insure that they clearly understood each task. A single experimental trial, consisting of 11 frequency plateaus with 10 cycles per plateau, lasted approximately 4 min. Rest

intervals were provided for the subject after each block of 5 trials, or upon request. The time for each of the three experimental sessions varied between 1 and 1.5 hours.

Within each trial, on one plateau chosen randomly, a single stimulus cycle was deleted ('missing stimulus perturbation'). Subjects were not informed that cycles would be missing, or what to do if such a situation arose, only, as mentioned above, to follow the metronome in the requested coordinative pattern. The response (or lack of response) during these missing pulse perturbations was separated from the main data set, recorded, and analyzed separately.

Following digitization of the data, in-house wave analysis software was employed to obtain the mean frequency of metronome and finger movement, the mean difference in real time between a given stimulus pulse and correlated flexion onset (reaction time,  $\Delta t$ ), the mean relative phase ( $\phi$ ) between the finger and the metronome, and the standard deviations of these variables at each frequency plateau in each of the conditions. These variables were then treated as individual scores in analyses of variance (ANOVA) with repeated measures for the 11 consecutive frequency plateaus;  $\Delta t$  and  $\phi$  were analyzed as separate dependent measures. For analysis of response distributions, the following bin widths were chosen: 50 msec for the stimulus–action interval ( $\Delta t$ ) and  $20^\circ$  for relative phase.

### 3. Results

#### 3.1. Accuracy of tracking

First, we established that subjects were capable of tracking the metronome over the specified frequency range (0.125 to 1.375 Hz) in all conditions. Pearson's product-moment correlations between actually produced and required frequency were calculated for all subjects. Following Fisher  $r$  to  $z$  transformation, the average correlations in the ascending frequency progression were  $r = 0.97$ ,  $r = 0.98$  and  $r = 0.95$  for reactive, synchronized and syncopated conditions, respectively. For the descending progression, the respective correlation values were  $r = 0.96$ ,  $r = 0.97$  and  $r = 0.95$ . These correlations demonstrate that subjects are almost always able to track the stimuli. However, under certain circumstances, such as at plateau boundaries and during transitions between behavioral modes, tracking is temporarily less precise. These issues will be considered in more detail in later sections.

### 3.2. Overall analysis

Performance in the reactive (Fig. 2A), synchronized (Fig. 2B) and syncopated (Fig. 2C) conditions, averaged across all subjects, is presented as a function of frequency and temporal progression (ascending and descending) for  $\Delta t$  and  $\phi$ . Main effects of condition ( $\Delta t$ :  $F(2,294) = 4130.44$ ,  $\phi$ :  $F(2,294) = 3051.03$ ), frequency ( $\Delta t$ :  $F(10,2940) = 1012.24$ ,  $\phi$ :  $F(10,2940) = 2.04$ ) and their interaction ( $\Delta t$ :  $F(20,2940) = 1022.05$ ,  $\phi$ :  $F(20,300) = 35.37$ ) were significant at

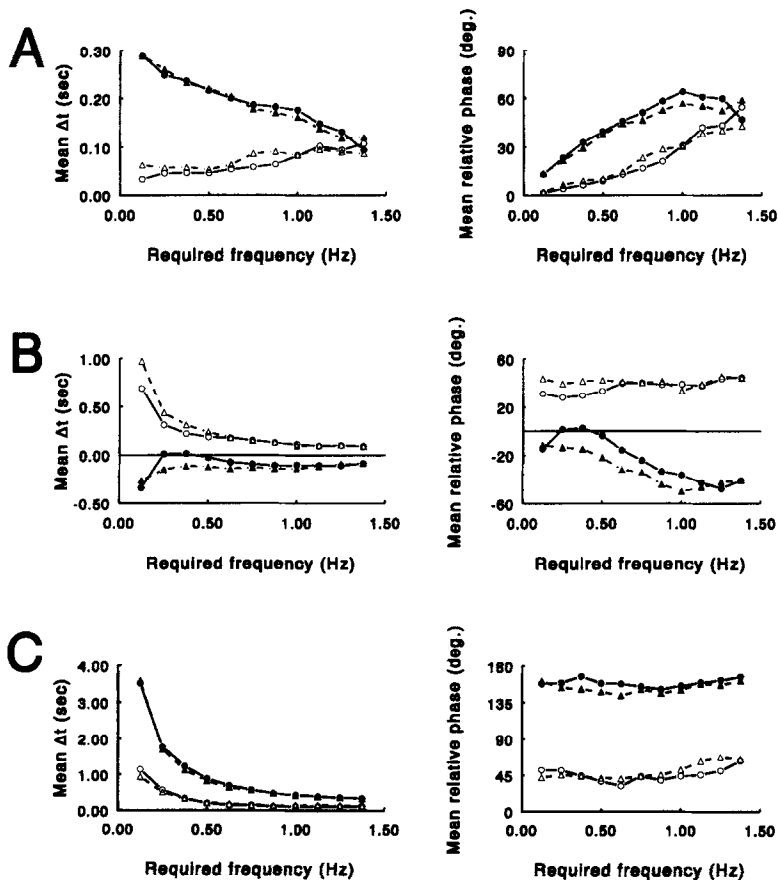


Fig. 2. Group mean data by frequency plateau, for both frequency progressions (ascending, solid lines and descending, dashed lines). Filled symbols are mean values, open symbols are SD. Mean and SD values are both measured on the same ordinate scale. (A) reactive, (B) synchronized, (C) syncopated. Left column,  $\Delta t$ ; right column, relative phase,  $\phi$ .



least at the  $p < 0.05$  level. The frequency progression effect was also significant ( $\Delta t$ :  $F(1,294) = 5.28$ ,  $p < 0.05$ ;  $\phi$ :  $F(1,294) = 9.06$   $p < 0.01$ ).

For variability measures (SD of  $\Delta t$  and  $\phi$ , respectively) there was a main effect of condition ( $F(2,294) = 209.57$  and  $70.79$ ,  $p < 0.01$ ) and frequency ( $F(10,2940) = 451.49$  and  $52.30$ ,  $p < 0.01$ ). The interaction of frequency and condition was also significant ( $F(20,2940) = 139.23$  and  $14.86$ ,  $p < 0.01$ ). As shown in Fig. 2, the frequency progression was not significant ( $F(1,294) = 3.31$  and  $2.63$ ,  $p > 0.05$ ). While reflecting overall, averaged behavior, the sources of these statistical effects become clearer with further, more detailed analysis, described below.

### 3.3. Reactive condition

In Fig. 2A (left), mean  $\Delta t$  (filled symbols) displays a systematic decrease as a function of frequency, accompanied by a corresponding increase in variability. The source of this effect becomes clear when we examine the distribution of  $\Delta t$  for the reactive condition. Fig. 3 presents distributions for ascending (solid lines) and descending (dashed lines) frequency progressions (for all of the distribution figures, the reader should follow the graphs from 0.125–1.375 Hz for the ascending, and from 1.375–0.125 Hz in the descending progressions). Note that the ascending and descending behavior is nearly identical. At the slowest stimulus frequency (0.125 Hz), we observe a sharp, unimodal population with peak value of approximately 240 ms. This agrees well with distributions of reaction times for discrete, serial visual stimuli reported by others (e.g., Wing and Kristofferson, 1973b). At the highest frequency (1.375 Hz), the main peak of the distribution has diminished, and the entire distribution is broader and more variable.

This variability is almost completely one-sided due to a substantial number of negative  $\Delta t$  values. Flexion-onsets in this case are actually *leading* the stimuli in time, and therefore, by definition, are no longer reactive. Note that responses are still highly correlated with the metronome; thus, the negative responses are not simply a result of loss of entrainment. Though it is hard to see from the graph, such anticipatory (stimulus leading) responses are present even at 0.5 Hz. However, by 0.875 Hz, these responses can be seen clearly (Fig. 3). The frequency range 0.5–0.875 Hz has some significance in the literature regarding human timing performance (Dunlap, 1910; Bartlett and Bartlett, 1959; Magdaleno et al., 1970; Mates et al., 1994; Pöppel et al., 1990). This frequency range falls within that which is reported to be where a rhythm can begin to be ‘felt’ or ‘perceived’ (Dunlap, 1910; Hah and Jagacinski, 1994; Magdaleno et al., 1970).

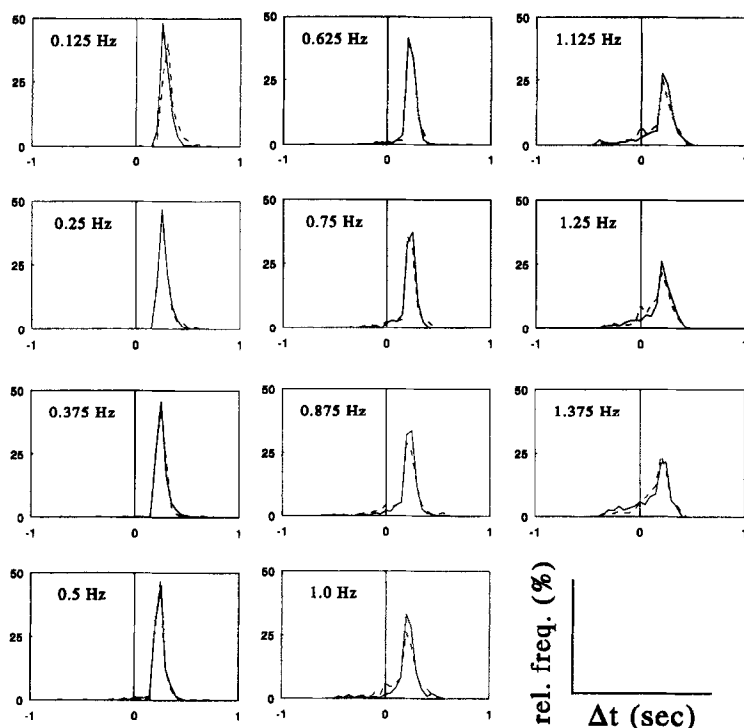


Fig. 3. Group  $\Delta t$  distributions over all metronome frequency plateaus tested for reactive coordinative pattern in both frequency progressions (ascending, solid lines and descending, dashed lines). Abscissa:  $\Delta t$  (sec). Ordinate: relative frequency of occurrence (%). In all of the distribution figures, for the ascending progression, frequency plateaus progress from 0.125–1.375 Hz in steps of 0.125 Hz, and in the descending progression, vice versa. Metronome driving frequencies are indicated on each graph. Note the progressive diminution in amplitude of the original peak at 0.23 seconds, and the increase of responses at smaller intervals. For  $\Delta t \leq 0$ , flexions are leading the metronome flashes, and are therefore anticipatory.

Fig. 4A-left (ascending frequency progression) and Fig. 4A-right (descending frequency progression) display individual trials in the reactive condition. These graphs provide some insight into the changes in the mean and distribution graphs. For instance, observe that the actual change occurring is often not smooth: at 1.0 Hz,  $\Delta t$  values change abruptly from positive (responses lagging stimuli) to predominantly negative (responses leading stimuli). Note also the fluctuations near the plateau boundaries, where the frequency is changed. A purely reactive system is not predicted to be affected by such perturbations. In Fig. 4A, ascending and descending temporal progressions appear to be quite different. Direct comparison between ascending and descending temporal progressions is not really valid, however, even though it may appear so. The reason

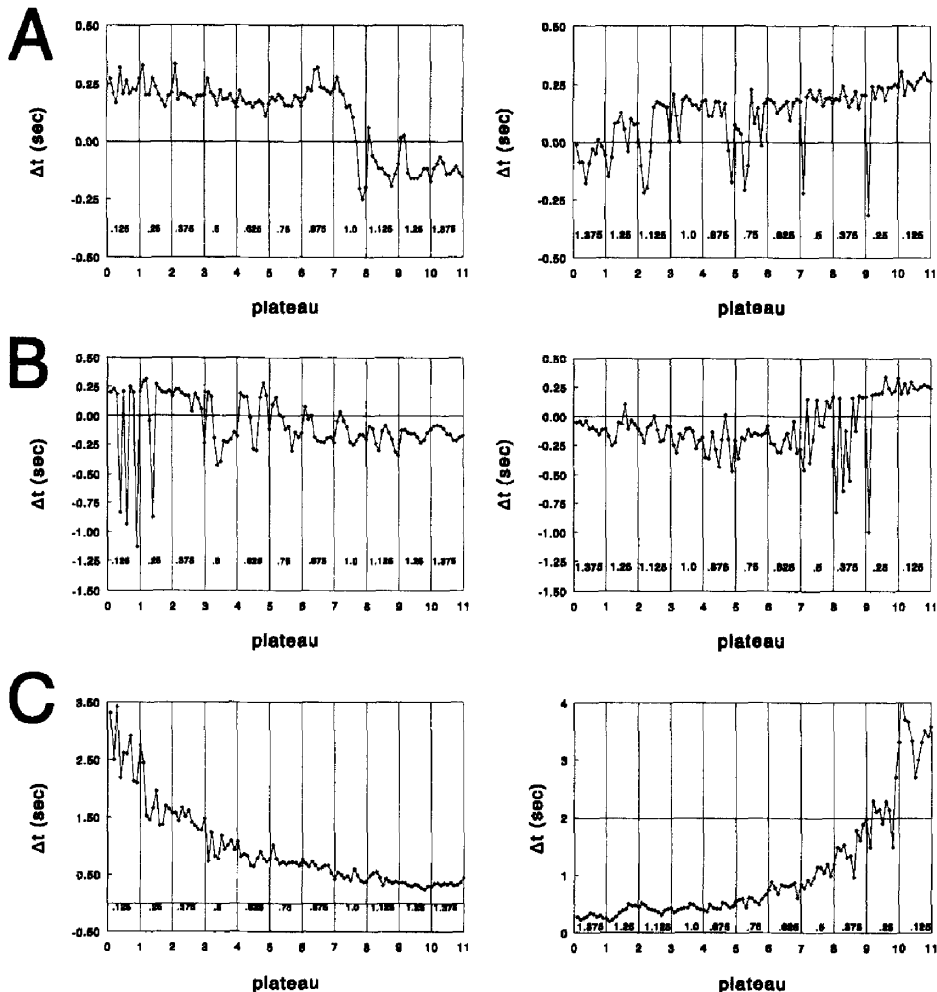


Fig. 4. Actual examples of individual time series for  $\Delta t$  in the three conditions in ascending (left) and descending (right) frequency progressions. Individual points represent single cycles. (A) reactive, (B) synchronized, (C) syncloned.

is that in the descending condition, subjects have to intentionally probe their ongoing pattern in order to determine if they can, in fact, react at the current frequency (see also Kelso et al., 1990).

Fig. 2A (right) displays mean relative phase data for the reactive condition. We observed a systematic increase in both the mean and variability. The increase in mean value (filled symbols) saturates around 1.0 Hz. The source of

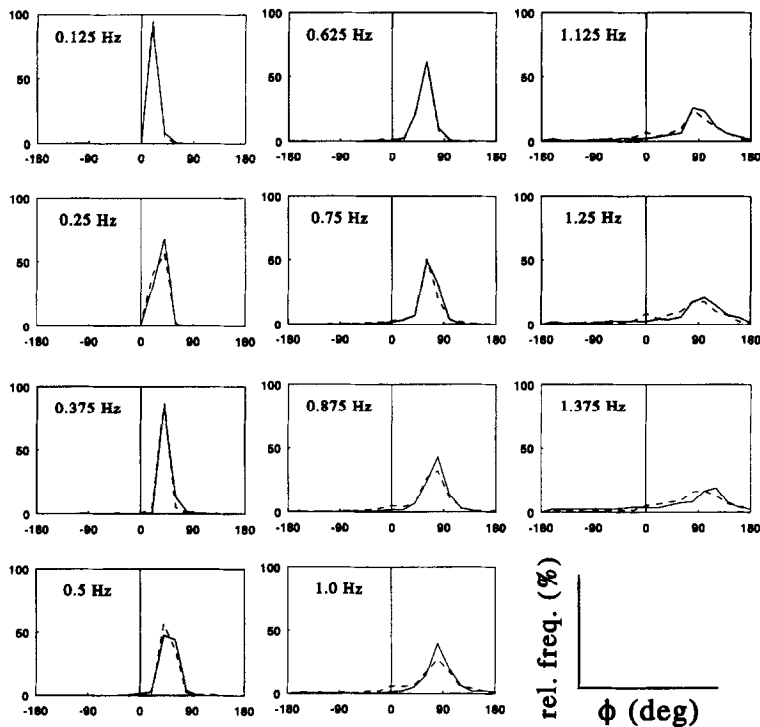


Fig. 5. Group  $\phi$  distributions over all metronome frequency plateaus tested for the reactive condition in ascending (solid lines) and descending (dashed lines) frequency progressions. Abscissa:  $\phi$  (degrees). Ordinate: relative frequency of occurrence (%). Note that for  $\phi \leq 0$ , flexions are leading the metronome flashes, and are therefore anticipatory.

this effect is made clear in Fig. 5, which displays relative phase distributions. These graphs show a progressive ‘smearing’ of the main peaks of both the ascending and descending distributions, and a progressive positive-going drift in the relative phase of the peak at higher frequencies. The drift towards larger relative phase values is an artifact of the relative phase calculation (i.e., since reaction times are nearly constant, during reactive behavior the relative phase is a function of the stimulus frequency only). Fig. 6A displays relative phase data for an individual trial for the reactive condition for ascending (left) and descending (right) frequency progressions. These graphs confirm the previous findings on  $\Delta t$ .

Fig. 7A presents the missing stimulus perturbation data for the reactive condition. In this graph, due to the small number of data points, ascending and descending frequency data are combined. The missing stimulus procedure

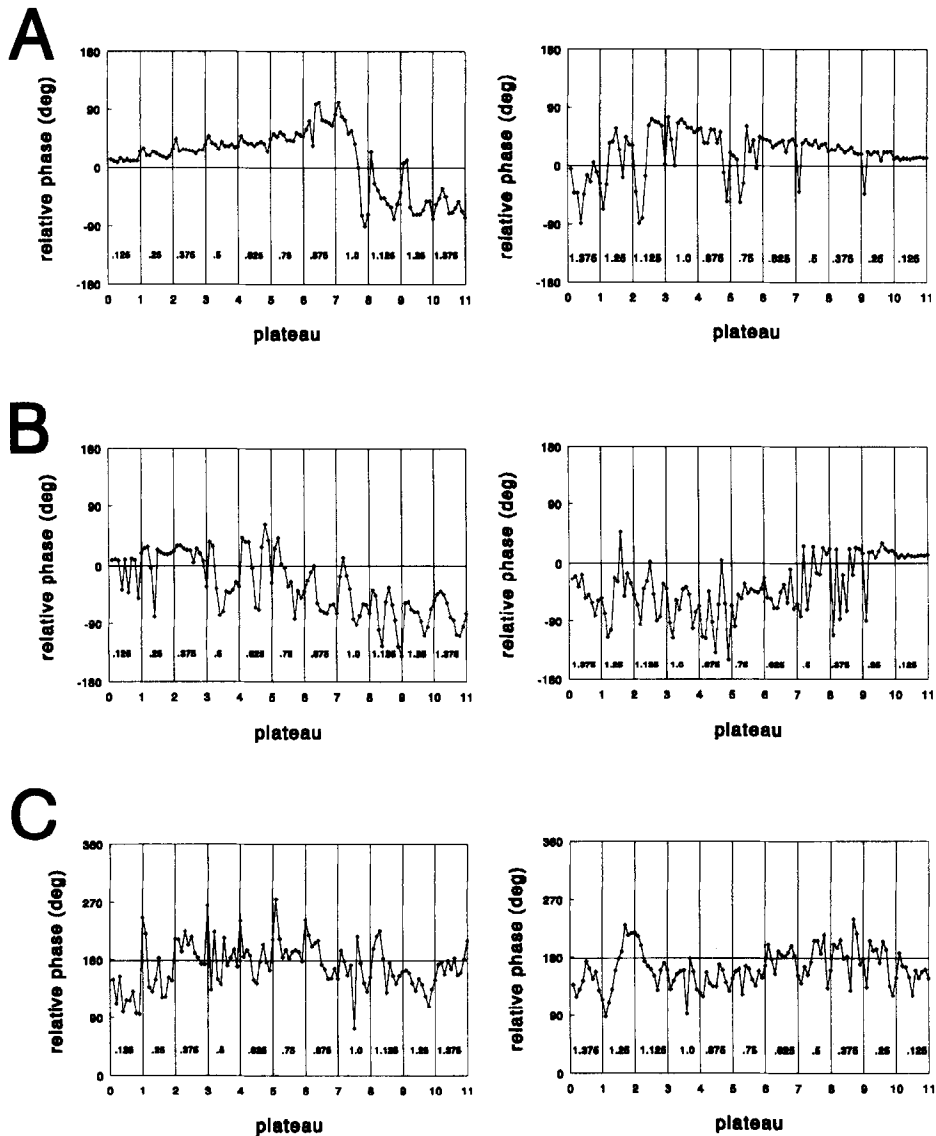


Fig. 6. Actual examples of individual time series for relative phase ( $\phi$ ) in the three conditions in ascending (left) and descending (right) frequency progressions. Individual points represent single cycles. (A) reactive, (B) synchronized, (C) syncopated.

results in two behaviors: no response (NR – subjects make no movement during the missing stimulus cycle) and false positive (FP – in this case, subjects produce a flexion during the missing stimulus cycle).

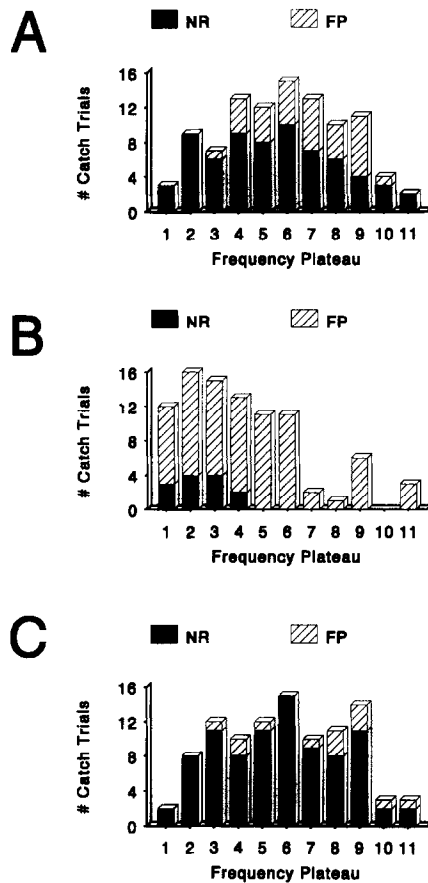


Fig. 7. Perturbation data, for all coordinative patterns: (A) reactive, (B) synchronized, (C) syncopated. NR, no response: subjects do not move in the time period of the missing stimulus. FP, false positive: subjects move as if the missing stimulus were actually present.

In the reactive condition, FP responses are not expected, since subjects should not produce a response without a stimulus. However, FP responses are clearly present, beginning as early as plateau 3 (0.375 Hz). FP responses are strong evidence that subjects are actually anticipating the stimulus pattern despite instructions to react to oncoming stimuli. Interestingly, there is evidence of FP responses in subjects that demonstrated no transitions from reactive to anticipatory responses. This suggests that these subjects were both reactive and anticipatory, indicating the possibility of coexistence of both coordination modes.

Taken together, these effects may be summarized as follows for the reactive condition. A systematic diminution of reaction time at increasing frequencies

exists (Fig. 2A), which is actually a mixture of two phenomena: (1) smooth changes in the individual subject's reaction times over the different frequencies (e.g., Wing and Kristofferson, 1973a); and (2) transitions from purely reactive to anticipatory behavior (Fig. 4 and Fig. 5). Since there exists individual variability in if and when such transitions take place, the averaged data (Fig. 2A) is naturally smeared.

### 3.4. *Synchronized condition*

Fig. 2B (left) displays mean  $\Delta t$  values for the synchronized condition. At slow stimulus frequencies, the behavior is dominated by responses lagging stimuli by about 250 ms. Then, we observe a progressive diminution of  $\Delta t$  starting at 0.375 Hz. Mean  $\Delta t$  values at low stimulus frequencies are somewhat misleading, due to large timing errors. Such 'jump-the-gun' type anticipatory errors have been reported by others (Pöppel et al., 1990; Mates et al., 1994). This can be seen in the  $\Delta t$  distributions: Fig. 8 displays the ascending (solid) and descending (dashed) distributions observed for the synchronized condition. At 0.125 Hz, the distribution is comprised of two components. The dominant component has a sharp population peak at approximately 250 ms, conspicuously similar to the distribution observed in the reactive condition at the same frequency (compare Fig. 3). The other component of the distribution has a long negative tail, which extends to  $-3$  sec (the graphs present data to  $-1$  sec). The first component is easily interpreted as simple serial reactions, the same as those observed in the reactive condition. At 0.125 Hz, subjects neither perform as if, nor report that they can, perceive an underlying pattern (Dunlap, 1910; Magdaleno et al., 1970). In this parameter region subjects either overestimate the time remaining to the next stimulus, which leads to a reaction, or grossly underestimate the time remaining, resulting in what appear to be poor guesses. The latter responses, which we refer to as 'anticipatory guesses', comprise the long negative tail in the distribution. While such responses can be technically described as anticipatory (preceding the stimulus in time), they are qualitatively different than those in which subjects can perceive a stimulus-response pattern, and should be so segregated. Lack of ability to synchronize with low frequency stimuli is supported by other studies (e.g., Bartlett and Bartlett, 1959; Dunlap, 1910; Magdaleno et al., 1970) which show that a subject's ability to synchronize or track a display decreases dramatically at inter-stimulus intervals greater than around 3 sec. Thus, when subjects cannot perceive an underlying pattern in a repetitive set of stimuli, but are requested to coordinate with one, they either make anticipatory guesses or react to the stimuli instead.

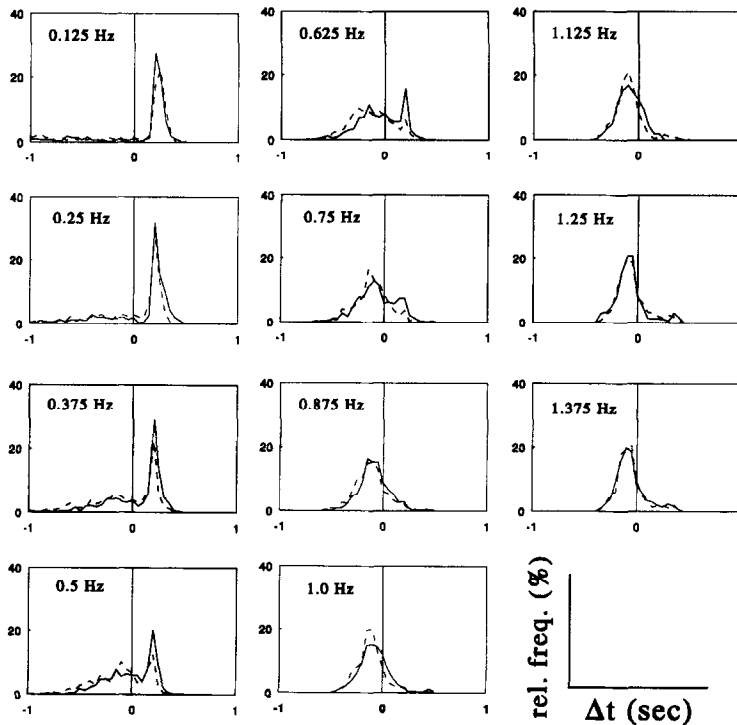


Fig. 8. Group  $\Delta t$  distributions for all metronome frequency plateaus tested in the synchronized coordinative pattern for both ascending (solid lines) and descending (dashed lines) frequency progressions. Abscissa:  $\Delta t$  (sec). Ordinate: relative frequency of occurrence (%).

At the highest stimulus frequency, 1.375 Hz, a new population of responses is evident, characterized by a somewhat larger variance and peak value just negative to zero. We identify this population as synchronized, or successful, anticipatory responses. The increased variance of this population (as compared with the sharp distribution at 0.125 Hz) is expected, since anticipatory responses are necessarily more uncertain than simple reactions. Similar to the reactive coordinative pattern, as the frequency increases from 0.125 Hz or decreases from 1.375 Hz, we observe a change in the distribution which eventually results in a new stable and qualitatively different distribution. Fig. 4B ( $\Delta t$ ) and Fig. 6B ( $\phi$ ) illustrate typical trials, and again demonstrate that the transition is not a smooth one. In Fig. 4B-left, one can easily distinguish reactive as well as anticipatory guessing behaviors in the first three frequency plateaus (0.125–0.375 Hz). This changes between 0.5–0.75 Hz to a new behavioral mode, which is predominantly negative with the exception of plateau boundary induced pertur-



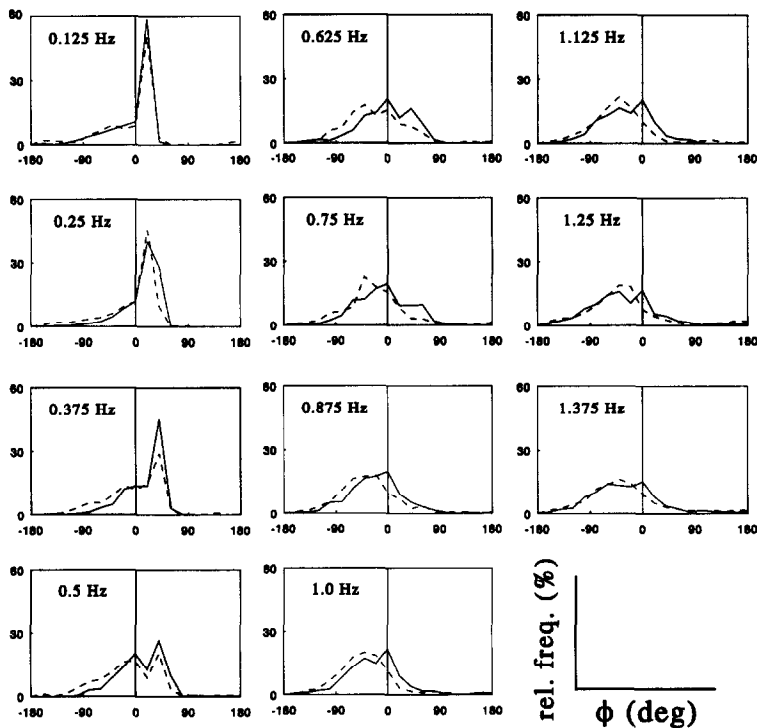


Fig. 9. Group  $\phi$  distributions for all metronome frequency plateaus tested in the synchronized condition for both frequency progressions (ascending, solid lines and descending, dashed lines). Abscissa:  $\Delta t$  (sec). Ordinate: frequency of occurrence (%).

bations. Interestingly, in this case, 0.5–0.75 Hz appears to be a transient parameter region, in which switching occurs between the dominant behaviors. Although this parameter region requires more detailed exploration, the present observations suggest a competition, or at least coexistence, between reaction and anticipation. Evidence for bistability is important, because details of the observed switching phenomenon are characteristic of different types of transitions. As we can see from the distributions (Fig. 8 and Fig. 9), the overall transition region is obvious, the change occurring between 0.5–0.875 Hz.

For the missing stimulus perturbations in the synchronized condition (Fig. 7B), though there is a propensity toward generation of FP responses in the slowest 4 frequency plateaus, there were cases of no response. If the subject was anticipating the metronome one would expect FP responses. However, the fact that this was not always the case suggests that the synchronization process was not well established at the lower frequencies.

### 3.5. Syncopated condition

Fig. 2C (left) shows the mean  $\Delta t$  data for the syncopated condition. In general,  $\Delta t$  values are negatively proportional to stimulus frequency. This is obviously related to the subject remaining 1:1 with the stimuli. The relative phase (Fig. 2C, right) remains nearly constant at all stimulus frequencies. Corresponding distributions for ascending and descending frequency progressions are displayed in Fig. 10 for  $\Delta t$  and Fig. 11 for  $\phi$ . The distributions in these conditions are different than those observed in the reactive and synchronized coordinative patterns, in that no obvious qualitative change occurs across the frequency range tested. At 0.125 Hz, we observe a single distribution for  $\Delta t$  with higher variance than observed in the other conditions, and a peak just under 4 sec. At each successive frequency plateau, including 1.375 Hz, this distribution narrows, its peak closely matching the required period. This is even clearer

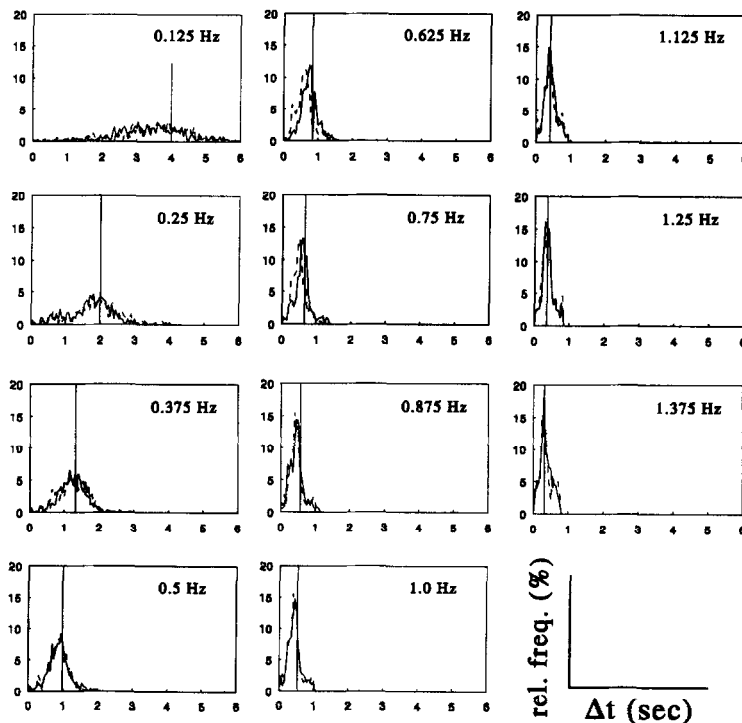


Fig. 10. Group  $\Delta t$  distributions for all metronome frequency plateaus tested in the syncopated condition for both ascending and descending frequency progressions. Abscissa:  $\Delta t$  (sec). Ordinate: frequency of occurrence (%).

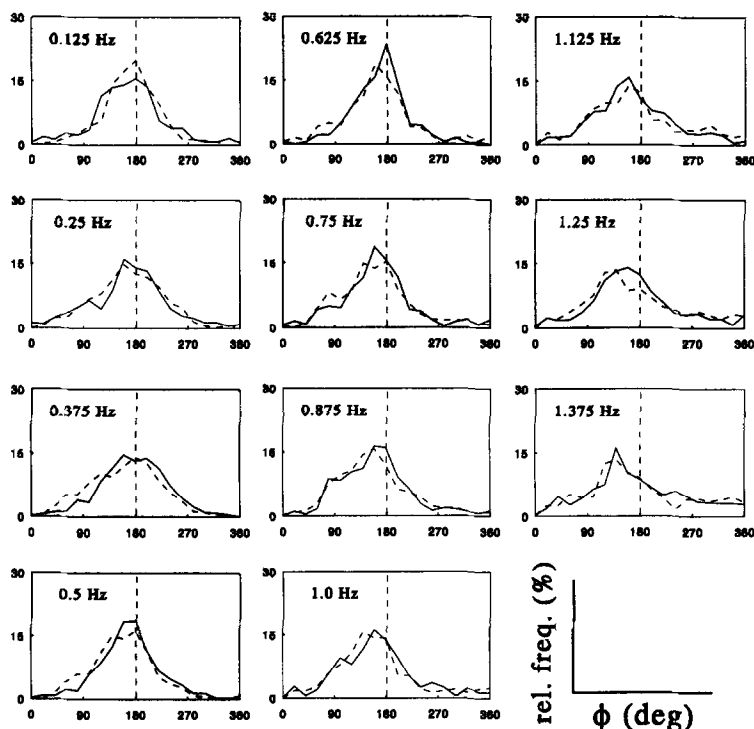


Fig. 11. Group  $\phi$  distributions for all metronome frequency plateaus tested in the syncopated condition for both ascending and descending frequency progressions. Abscissa:  $\Delta t$  (sec). Ordinate: frequency of occurrence (%).

in the relative phase graph (Fig. 11). Here we see that the group performance centered around  $180^\circ$  throughout the trial. Note that transitions were seldom observed in the syncopated condition. This is interesting especially since transitions were always seen in the synchronized condition, and it has already been demonstrated that at higher stimulus frequencies, subjects display several different qualitative transitions from the syncopated to other coordinative modes (Kelso et al., 1990). However, in the Kelso et al. study the parameter range was much higher (up to 3.5 Hz) than that employed here. Moreover, no syncopate-to-synchronize transitions were observed below 1.45 Hz in their study.

There are several further points worth mentioning about the syncopated condition. First, since subjects are requested to provide flexion-onsets halfway between stimulus pulses, the effective wait period is half of that for the synchronized condition. For instance, at the 0.125 Hz frequency plateau, subjects were required to wait roughly 8 seconds between consecutive metronome

flashes before providing a flexion in the synchronized condition, but only 4 seconds to correctly place the flexion in the syncopated condition at the same stimulus frequency. Second, while responses in the synchronized condition usually precede the stimulus in a truly anticipatory fashion, the syncopated condition may contain a reactive component, since flexions are in advance of the last stimulus and precede the current stimulus by approximately the same amount of time. This possible mixture of reactive and anticipatory features, as well as the unavoidable decrease of 'wait for next stimulus' time may explain the observed syncopation data at slower frequencies.

The missing stimulus perturbation data for the syncopated condition is shown in Fig. 7C. It is reminiscent of the behavior observed in the reactive condition (Fig. 7A). Very few FP responses were observed overall, those few observed beginning at stimulus frequencies of 0.375 Hz and higher.

#### 4. Discussion

Using a methodology in which the stimulus frequency was continuously varied over a broad range, we report that spontaneous, involuntary transitions between reactive and anticipatory perception-action coordinative patterns occur at critical values of stimulus frequency. These transitions are bi-directional, and correspond to changes in behavior from responding to a stimulus pattern (reactive), to responding with a stimulus pattern (anticipatory), and vice versa. Importantly, both behaviors are stable in some range of the parameter values studied, and more variable in others. Taken together, these findings suggest that reaction and anticipation are stable modes or states of a single multifunctional system, rather than separate behaviors. It is interesting to note that Michon (1967) stated that explanations of temporal aspects of behavior are similar for time perception and for timing of discrete response and rhythmic performance. Actually there is recent evidence supporting the existence of neural multifunctionality in certain invertebrates (e.g., Schöner and Kelso, 1988, for review; Mpitsos et al., 1988). Most studies, however, avoid the multifunctionality issue entirely. The principal emphasis is on time itself, for example, defining a specific interval of time over which optimal integration occurs between the stimulus and corresponding motor act. Here however, the temporal interval is a tunable parameter that serves to distinguish different modes of behavior. Moreover, whether a 2–3 sec interval is optimal for temporal binding, defines the subjective now, or constitutes a maximum information processing time is, in the present view, somewhat equivocal. In our approach, whether 2–3 sec is optimal

or not depends entirely on the underlying dynamics. Although subjects may anticipate or synchronize well within this interval, in other contexts, as we have shown, such anticipation can be maladaptive.

In past work, both reactive and anticipatory timing phenomena have been studied in isolation. Typical reaction time experiments avoid or eliminate anticipatory responses, while synchronization studies may treat reactions as positive timing errors. We contend this separation is not well grounded: it is unknown whether or not, for instance, the timing process(es) responsible for the production of successful anticipatory performance are different than those responsible for simple reaction time behavior (utilize different neural pathways, neurotransmitters, brain areas, etc.).

Consideration of the problem of reaction and anticipation leads to some paradoxical conclusions, as follows: While a reactive subject can coordinate (follow, track) a random pattern, which is a necessary skill when the subject is navigating a novel environment, the anticipatory subject generates anticipatory errors, which can be maladaptive. In this case, the reactive mode is clearly the more viable biological strategy. On the other hand, reactive delays can be maladaptive in many circumstances, such as in flight or combat, batting or base stealing in professional baseball, or in photography, where anticipatory responses are actually mandatory for even nominal performance.

In our study, reactive coordination could be considered absolute, or mode-locked, coordination, and synchronization, relative coordination (von Holst, 1939), if we base our conclusions upon response distributions. This much seems evident: in the reactive case, responses are 'caused' by each stimulus, while in the synchronized case, subjects actually respond in advance of the stimulus. However, considering the missing stimulus perturbation data, we see that anticipation (in this case, synchronization) seems to be a mode-locked, or absolutely coordinated, behavior, because subjects produce responses in the absence of a stimulus which are placed in time where they would have been if the stimulus were present. In contrast, the reactive subject does not make false positive responses. How can consideration of these problems along with the current data help us to understand the behavior?

First, we see that, at least for our subjects, successful reaction and anticipation seems to be constrained to frequency ranges which are appropriate for such behavior. That is, stimuli which are too slow for a pattern to be detected should be, and are, reacted to, since attempts at synchronization lead to gross, possibly unfavorable outcomes. On the other hand, when stimuli are provided in a range in which a pattern may be detected, the system switches to an anticipatory mode, sparing the subject from unnecessary reaction delays, which also could

lead to unfavorable outcomes. Next, we see that both modes seem to be flexible. For instance, while outside the parameter range in which a pattern can be detected, the subject is still able to generate anticipatory guess responses, even though reactivity is the indicated, or stable mode. Transitions between behavioral modes occur at different (but related) frequencies and cycles between and within subjects; they occur in both ascending and descending frequency progressions. Reactions occur with unexpected changes in frequency, and last until the subject comes into synchrony with the new frequency.

We have shown that reactive and anticipatory behavior can be understood as two complementary modes of a single dynamical system. This does not mean that different brain areas may not be differentially recruited for these processes. In fact, there is evidence that they might be. For example, Fuchs et al. (1992) show that synchronization and syncopation patterns occupy frontal and prefrontal brain regions often associated with anticipatory behavior, whereas purely reactive conditions are mediated by classical sensory and motor cortical areas. However, paradigms such as the one used here may elucidate how information is routed selectively from one brain area to the other. Reaction–anticipation then is subject to the intrinsic dynamics of the particular coordinating system, and is predicted to display qualitatively similar behavior in all such coordinating systems. This has many ramifications for experimental design and our notions about how biological coordination works, since much coordination includes reactive and anticipatory effects. Perhaps most importantly for neurobehavioral dynamic systems, *coordination* may be a more relevant and useful concept than *causality*.

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