

PSYCHOMETRIC COMPARISONS BETWEEN HUMANS AND RHESUS MONKEYS ACROSS TIME PRODUCTION TASKS

Hugo Merchant, Wilbert Zarco, Luis Prado and Ramón Bartolo

Instituto de Neurobiología, UNAM campus Juriquilla, Querétaro 76230 México

ABSTRACT

Timed motor behavior is at the essence of higher-level cognition, from planning and collision avoidance to speech. This study aims to provide some evidence for graded continuity of timed motor behavior across primate species. Motor timing performance was compared between twenty human subjects and three Rhesus monkeys during both a synchronization-continuation and a single interval production task. These tasks involved tapping on a push-button to produce the same set of intervals (range: 450 to 1000 ms), but they differed in the number of cyclic repetitions (single vs. multiple) and the modality of the stimuli (auditory vs. visual) used to define the time intervals. The data showed that the variability and accuracy of rhesus monkeys was equivalent to that of human subjects during both the production of single intervals and the tapping synchronization to a metronome. Nevertheless, the monkeys' asynchronies were around 300 ms, suggesting that these animals were not able to synchronize their movement to a sensory metronome as humans do. In addition, human subjects were more accurate than monkeys and showed less timing variability. This was especially true during the self-pacing (continuation) phase of the multiple interval task, a behavior that may be related to complex temporal cognition, such as speech and music execution.

1. INTRODUCTION

Temporal information spanning in the hundreds of milliseconds is a key element during speech production and comprehension (Shannon et al. 1995), music performance (Janata & Grafton, 2003; Mauk & Buonomano, 2004), and survival motor actions, such as target interception and collision avoidance (Merchant & Georgopoulos, 2006; Merchant et al. 2009). The interpretation of the beats with a rhythmic pattern allows people to move and dance in time to music. In turn, the way we move may influence our perception of musical rhythm (Phillips-Silver & Trainor, 2005). As in music, there is a spectral and temporal structure in speech necessary for successful word articulation and recognition (Diehl et al. 2004). The ability to accomplish such precisely timed movements suggests the presence of a central timing mechanism. A number of experimental approaches from psychophysics to functional neuroimaging have been used to disentangle the underlying mechanisms of a timing system (Mauk & Buonomano, 2004). Three main findings can be extracted from an extensive literature: 1. Weber's law holds for a differentiated time window, from 200 ms to 2000 ms, after that range Weber fraction begins to increase proposing a break-point on how information is processed (Grondin, 2001). 2. During

sensorimotor behavior guided by a cyclic external cue in human subjects, there is a behavioral transition between predictive and reactive responses (asynchronies) around 1600-2000 ms, stressing the discontinuity of the internal mechanism of sensorimotor anticipation (Miyake et al. 2004; Shelhamer, 2005). 3. Different cortico-basal ganglia loops are recruited while human subjects perform timing tasks on different time scales. In the sub-second range a medial frontal cortex-striatal circuit is consistently involved, whereas supra-second intervals recruited prefrontal and parietal areas (Lewis & Miall, 2003; Macar et al. 2006). Regarding the second point, a question that remains is whether the entrainment skill and precise temporal coordination of movements is exclusive to humans or it is also observed in animal species with a complex and flexible behavioral repertoire. Recently, it has been proposed that only animals that showed some sort of vocal mimicking are able to synchronize their movements to external periodicities (Patel 2006). Indeed, the species of birds that show vocal mimicking can spontaneously entrain their movement to different rhythms (Schachner, 2009; Patel, 2009). In the present study we characterized the tapping behavior of macaques, a close evolutionary relative of humans that do not show vocal mimicry but have a complex behavioral repertoire. We provide a psychophysical description of the similarities and differences in motor timing performance between both species during two time production tasks. The results have been published in detail in a previous paper (Zarco et al. 2009), and suggest that Rhesus monkeys are a valid animal model to study the neurophysiological mechanisms of motor timing. Interestingly, our findings also confirm that animals with no vocal mimicry cannot synchronize their movement to a sensory metronome.

2. METHODS

The methods and tasks are described in detail elsewhere (Zarco et al. 2009; Merchant et al. 2008). Briefly, 20 human subjects (10 M and 10 F), mean (SD) age of 26.5 (2.5) years were tested in this study. They were right-handed, had normal or corrected vision. Each subject volunteered and gave informed consent for this study, which complied with the Declaration of Helsinki and was approved by the National University of Mexico Institutional Review Board. Three naive male monkeys (*Macaca mulatta* 5-7 kg) were used. All experimental procedures with the animals were approved by the National University of Mexico Institutional Animal Care and Use Committee and conformed to the principles outlined in the Guide for Care and Use of Laboratory Animals (NIH, publication number 85-23, revised 1985).

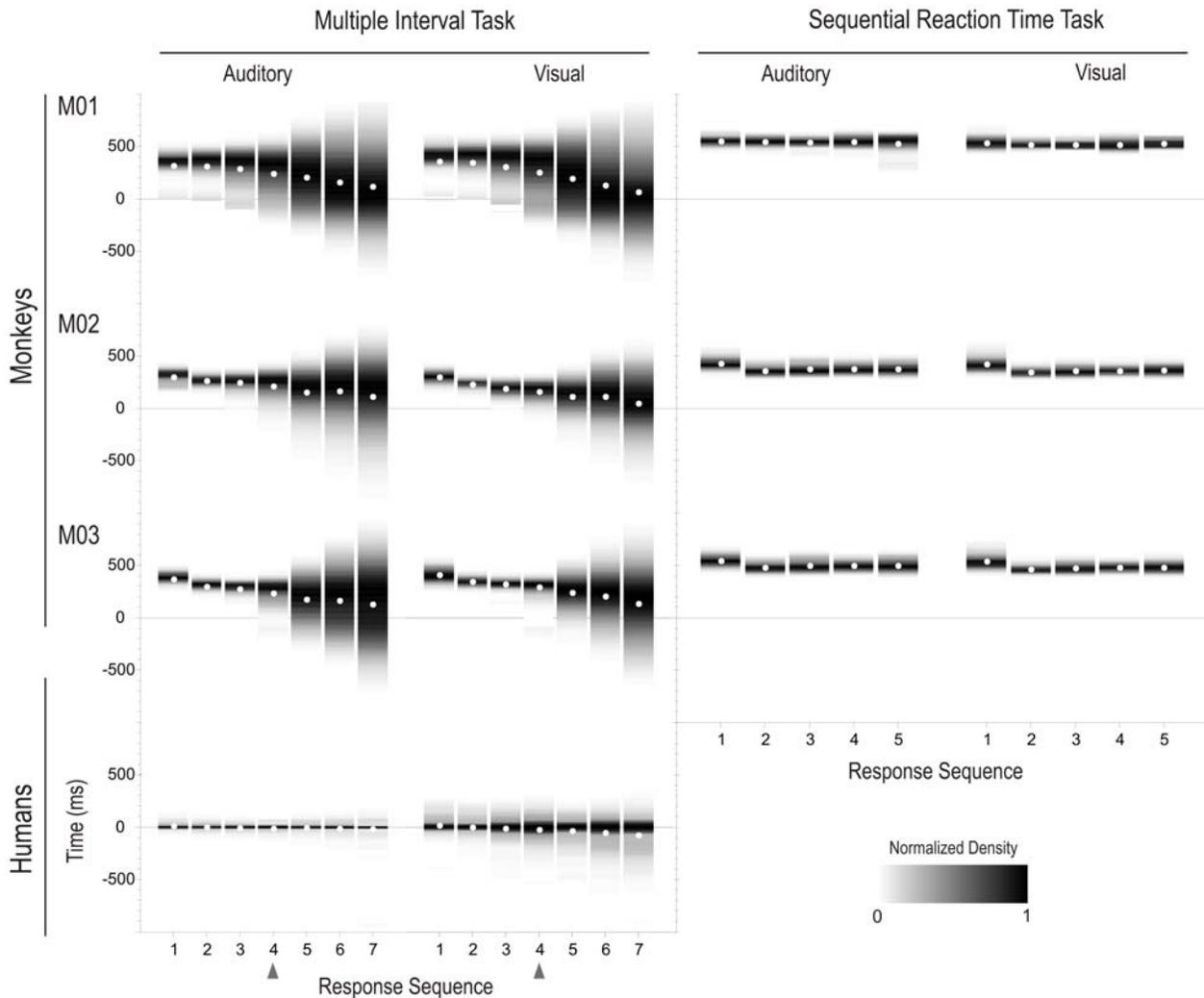


Figure 1: Left. Distributions of mean asynchronies as a function of the response sequence in the MIT. The first four taps correspond to the synchronization and the last three to the continuation phase. Data of the three monkeys are shown on the first three rows and the overall human subject behavior is shown on the bottom row. Right. Distributions of reaction times as a function of the response sequence in the SRT for the three monkeys. The auditory and visual interval marker conditions are depicted in the left and right subpanels, respectively.

Human subjects were seated comfortably on a chair facing a computer screen (Dell Optiplex 19") in a quiet experimental room and tapped on a push-button (#7717, Dassel MN, USA) during the production tasks. The subjects could not see their own hand during tapping. Monkeys were seated in a primate chair in a sound-attenuated room facing a computer screen. The animals tapped on the same type of push-button with one hand. The monkeys started each trial in the tasks by putting their working hand on a horizontal key that was placed next to the push-button. The stimulus presentation and the collection of behavioral responses were computer-controlled. Auditory stimuli were presented through noise-canceling headphones (Sony, MDR-NC50) or two equidistant front speakers for humans and monkeys, respectively.

2.1 Tasks

Task 1: Production of multiple interval task (MIT)

At the beginning of the trial, stimuli were presented with a constant inter-onset interval equal to the selected target interval. Subjects were required to push a button each time a stimulus was presented, which resulted in a stimulus-movement cycle. The subjects started to press the button when they were ready to start the synchronization phase. After four consecutive synchronized movements the stimulus is turned off, and the subjects continued tapping with the same interval for three additional intervals. Monkeys received a reward if each of the intervals produced had an error < 35% of the target interval. For human subjects feedback was displayed on the screen as the mean intertap interval and standard

deviation for the continuation phase. Throughout the experiment, trials were separated by a variable inter-trial interval (1.2 to 4 sec). For both human subjects and monkeys the auditory stimuli were pure tones (33 ms, 2000 Hz, 65 dB). Visual stimuli were red 4-cm side squares presented in the center of a black background computer screen for 33 ms. The target intervals were 450, 550, 650, 850, or 1000 ms, and were chosen pseudorandomly within a repetition or trial. Ten repetitions were collected for each interval for a total of 300 produced intervals.

Task 2: Production of a single interval task (SIT)

For each interval, there was a training and an execution period. In the training period, a target interval (two stimuli separated by a particular target interval) was presented at the beginning of the trial. Then the subject tapped twice on the push-button to produce the same interval. This was repeated for 5 training trials, after which the subject entered the execution period, where he/she produced another 10 single intervals, each in response to a go signal that appeared on the screen. In the case of monkeys, each duration interval was associated with a particular stimulus feature (i.e. 450 ms with a blue square) so that during the execution period the go signal was a stimulus, which had been linked to the production of a specific interval during the training period. Monkeys were rewarded following the same rules described in Task 1. Again, feedback was displayed on the screen for human subjects, indicating the mean intertap interval and SD across trials of the same target interval during the execution period. Throughout the experiment, trials were separated by a variable 1.2 to 4 sec inter-trial interval. In this task we only tested four target intervals: 450, 650, 850, or 1000 ms. The same auditory and visual stimuli as in the MIT were used in human subjects. Overall, a total of 60 produced intervals (40 for the execution period) were collected.

3. RESULTS

3.1 MIT

Asynchronies. Initially we compared the mean asynchronies for humans and monkeys in the MIT. The asynchronies are defined as the time difference between the stimulus onset and the tap onset. Figure 1 shows that human subjects were able to synchronize their behavior to the metronome in the synchronization phase with negative mean asynchronies (white dots), particularly in the visual modality. In contrast, the asynchronies in monkeys were positive and around 300 ms across intervals. A repeated-measures analysis of variance (ANOVA) was carried out in which species (monkeys and humans) was the between-subjects variable, the interval duration and marker modality (auditory and visual) were defined as within-subjects variables, and mean asynchronies was the dependent variable. The results only showed significant main effects for species ($F(1,21) = 464.2, p < 0.0001$). These findings indicate that monkeys were not able to synchronize their tapping behavior to the sensory metronome as human subjects do. We also compared in the monkeys the mean asynchronies of the MIT with the reaction times of a sequential reaction time task (SRT), in which the animals performed five tapping movements in response to five stimuli with random (600-1400 ms) inter-onset intervals in order to

receive a reward in each trial (Figure 1). A repeated-measures ANOVA using the asynchronies (MIT) and the response times (SRT) as dependent variable and task and modality as within-subjects variables, revealed significant main effects for task ($F(1,2) = 143.02, p = 0.007$), but not for modality ($F(1,2) = 0.188, p = 0.707$) or the task-conditions x modality ($F(1,2) = 10.9, p = 0.081$) interaction. Therefore, these findings suggest that although the monkeys were not able to synchronize their behavior to external cues, their mean tapping responses in the MIT (~300 ms) were shorter than the reaction times in the SRT (~480 ms), and hence, showed some level of predictive movements during the synchronization phase.

Variability. Figure 2 shows the overall SD (mean \pm SEM) for human subjects and monkeys during the synchronization and continuation phases of the MIT, for the visual and auditory marker conditions. The results of the corresponding repeated-measures ANOVA showed significant main effects for species ($F(1,113) = 17.58, p < 0.0001$), modality ($F(1,113) = 19.52, p < 0.0001$), and phase ($F(1,113) = 18.42, p < 0.0001$), as well as a significant effect for the species x phase ($F(1, 113) = 23.4, p < 0.0001$), and species x modality ($F(1, 113) = 14.5, p < 0.0001$) interactions. These results indicate that in both phases of the MIT, the overall variability was larger in monkeys than in humans, and it was also larger for visual than for auditory markers. In addition, the interaction effects demonstrated that humans showed a larger increase in temporal variability in the visual condition than monkeys, and that whereas humans showed a decrease, monkeys showed an increased variability in the continuation phase when compared to their own synchronization phase. In general, two main conclusions can be reached from these results: (1) monkeys showed a larger temporal variability than human subjects, particularly in the continuation phase; (2) SD was larger in the visual than in the auditory condition, and this modality difference was more pronounced in human subjects.

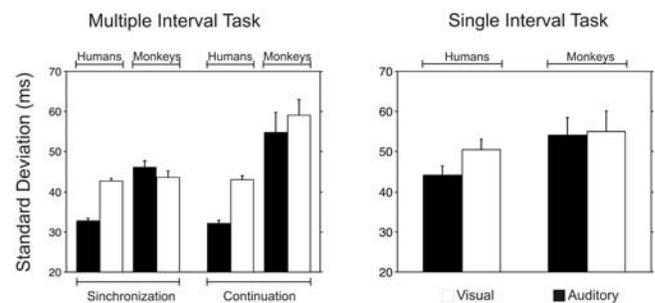


Figure 2: Standard deviation (Mean \pm SEM) of the inter-response intervals for the two species, the two marker modalities (auditory = black bars; visual = open bars), the two MIT phases (left) as well as the SIT (right).

Accuracy. The constant error can have different values; zero reflecting perfect performance, and positive and negative values reflecting over- and underestimation, respectively. The mean constant error of human subjects and monkeys is reported in Figure

3. The MIT constant error was negative across all conditions and species. The results of the ANOVA showed significant main effects for species ($F(1,113) = 42.6, p < 0.0001$), modality ($F(1, 113) = 11.1, p = 0.001$), and phase ($F(1, 113) = 24.1, p < 0.0001$). In addition, significant effects were found on the species x phase interaction ($F(1,113) = 24.4, p < 0.0001$). These results indicate the following: (1) human subjects were more accurate than monkeys across conditions; (2) both species were more accurate in the auditory condition, producing shorter intervals in the visual condition; (3) constant error increased in the continuation phase, particularly in monkeys.

3.2 SIT

Variability. The overall SD (\pm SEM) in the SIT is also plotted in Figure 2. It is clear that the temporal variability was similar between species and modalities, although there was a slight decrease in SD for the auditory condition in human subjects. Indeed, the ANOVA revealed no significant main effects or interaction on species and modality. Consequently, this results indicate that monkeys can produce single intervals with a similar variability than humans.

Accuracy. Just as in the MIT, the constant error was smaller in human subjects than in monkeys during the SIT, as illustrated in Figure 3. The corresponding ANOVA showed significant main effects on species ($F(1,90) = 26.9, p = 0.003$), but not for the modality ($F(1,90) = 1.16, p = 0.284$) nor the species x modality interaction ($F(1,90) = 0.54, p = 0.462$). Hence, these findings are in accordance with the main observation of the MIT, namely, that human subjects were more accurate than monkeys.

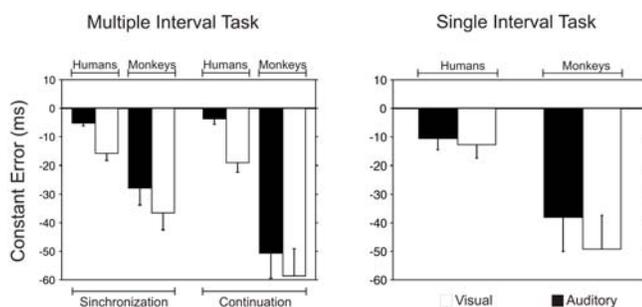


Figure 3: Constant error (Mean \pm SEM) for the two species, the two marker modalities, and the two phases in the MIT as well as the SIT. Conventions are the same as in Figure 2.

3.3 Comparing MTI and STI

An ANOVA was performed with the temporal variability as dependent variable, species as between-subjects variable and task (continuation in MIT vs. SIT) and modality as within-subjects variables. The results only revealed a significant main effect on species ($F(1,90) = 22.7, p < 0.0001$). Hence, these results

underscore the differences in temporal performance between the two primate species.

4. DISCUSSION

The results suggest the following points: (1) During the production of single intervals and the production of multiple intervals cued by a sensory metronome, the monkeys' timing variability was similar to that of human subjects. (2) In contrast to human subjects, monkeys did not synchronize their tapping to the sensory metronome. (3) During the continuation phase of the MIT, human subjects showed a decrease, whereas monkeys showed an increase in variability with respect to the synchronization phase. (4) In both tasks, the timing variability and constant error was larger for visual than auditory markers, particularly in humans.

These observations demonstrate that the accuracy and variability in producing single temporal intervals in the sub-second scale are similar between the two primate species. However, a large inter-species difference emerges when the MIT performance is compared. Monkeys showed large variability and error during continuation phase and were not able to synchronize their tapping to a metronome. Indeed, humans were exceptionally good at synchronizing their responses to an external periodic stimuli, with typical negative mean asynchronies around -8 ms. In contrast, monkeys showed positive asynchronies (~300 ms) during the execution of the MIT, that nevertheless had a predictive component when compared with the SRT (~480 ms). This inability of a non-human primate to entrain to an external periodic stimulus was predicted by the 'vocal learning and rhythmic synchronization' hypothesis (Patel, 2006). According to it, synchronization capacity partially shares the neuronal network for complex vocal learning, given that both behaviors require a perceptuomotor coupling during learning and execution. This prediction has been supported by recent studies that showed that only species with vocal mimicry abilities are able to synchronize their movements to external rhythms (Schachner et al. 2009; Patel et al. 2009). On the other side, it has been shown that preverbal infants can produce rhythmic movements when listen to various music excerpts, including isochronous drumbeats but not to speech (Winkler et al. 2009; Zentner et al. 2010). Hence, it is possible that in addition to speech, other complex behaviors that we share with our non-human primate relatives can have a functional overlap with the temporal control of movement. One could speculate that the brain mechanism involved in motor timing was a target of natural selection because it facilitates the alignment of movement patterns with environmental regularities of biological significance. For example, single interval timing and production may be a temporal processing primitive shared across species. Accordingly, our results leave the possibility of a graded continuity of timed motor behavior across primate species, reaching a summit in humans during speech and music performance. Comparative studies using other primate species can be useful for understanding the evolutionary roots of our most distinctive abilities, paving the way for investigations into the neural mechanisms of time processing.

5. REFERENCES

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