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# TOWARDS A COMPARATIVE PSYCHOLOGY OF TIMING BEHAVIOR

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After outlining of the evolution of comparative psychology of time, this paper presents hypotheses, experimental strategies and recent data relevant to between-species comparisons. The animal-human generalizability issue is briefly discussed, as well as the role of language and the relevance of developmental studies to animal-human comparisons in particular. The paper argues for the development of an integrative theory of timing, taking both comparative and developmental aspects of behavior into account.

The estimation of time in non-human animal species has been extensively studied over the past decades, especially since operant procedures were developed. The available literature amounts to several hundred papers and interest has been stimulated by the fact that timing behavior can be described by empirical laws, such as the power and the Weber's law (Catania, 1970; Platt, 1979), and also by the development of formal models of hypothesized internal clocks, such as Church's information processing model of timing (1984).

Even though numerous papers have been devoted to animal timing, few of them have dealt with the study of cross-species differences and similarities. The publication of "Time in Animal Behaviour" by Richelle and Lejeune in 1980 showed that to that date less than thirty species had come under scrutiny. Furthermore, very few studies compared two or more species within a similar experimental setting. A survey of 175 papers published between 1953 and 1977 revealed that most studies used common laboratory animals such as pigeons and rats. The choice of the species and the experimental strategy depended more on availability and cost criteria than upon the theory of biological evolution. Comparison between humans and animal species was also neglected, with only a few papers specifically taking this topic into account (Lowe, 1979). Finally, the developmental dimension within inter-species comparisons was completely ignored.

What has changed since 1980? The number of species under scrutiny has not significantly increased. Publications where two or more species were compared in a similar experimental setting have been as rare as

before, and their choice has still mostly depended on arbitrary criteria. However, the experimental strategy followed in a few experiments has borne some relation to the theory of evolution. The comparison between human and animal species under similar experimental settings has also gained prevalence over comparing animal species (Wearden, 1991). Finally, the developmental dimension within between-species comparisons has fueled a discussion that is far from finished today.

In summary, the comparative psychology of time is at present less zoocentric, i.e., concerned with the evolutionary scaling of timing abilities than anthropocentric, i.e., concerned by the generality of timing mechanisms at work in the human species. It thus resolutely steps behind the banner of comparative cognition in general, which focusses on the phylogeny of intelligence, the similarity between cognitive processes in animals and humans, and the specific role of language (Wasserman, 1993).

## TIMIND AND EVOLUTION: SOME HYPOTHESES, STRATEGIES AND RESULTS

In parallel with the emphasis on animal-human comparisons, attempts have been made to elaborate hypotheses and experimental strategies suited to the study of the relationship between timing abilities and evolution. Three hypotheses have been formulated (Richelle, Lejeune, Fery & Perikel, 1985). The first is the egalitarian or reductionist hypothesis, according to which all species, including humans, are endowed with the same timing aptitude. A second proposal is the evolutionary or phylogenetic hypothesis suggesting that timing aptitudes follow a trend in parallel with the increase in some general learning ability or to the complexity of the central nervous system. Thirdly, there is the ethological hypothesis which relates the species-specific aptitude to the environmental conditions under which it has evolved. The evolutionary and ethological hypotheses both postulate inter-species differences. However, they differ about the relationship that might be found between evolution and progress. Whereas the former relies on some a priori *scala naturae*, the latter does not propose any necessary correlation between the position of the species and the degree of complexity, refinement or flexibility of its adaptation to time.

Operant procedures based on the law of effect have been adapted to the study of the comparative psychology of timing. The techniques used can be subdivided in two main categories: temporal discrimination

and temporal regulation. In the former, the subject has to judge the duration of some exteroceptive stimulus. In the latter, time estimation is expressed via the distribution of behavior in time. For example, in the Differential Reinforcement of Low rate schedule (DRL), a reinforcer will be obtained only if successive responses are separated by a specified delay. A variant of this procedure, the Differential Reinforcement of Response Duration schedule (DRRD), reinforces the duration of the operant response, instead of response spacing. The proportion of Inter-Response-Times (IRTs) or response durations close to the schedule-specific target duration increases progressively with training, at the expense of too short (unreinforced) or too long reinforced but time-wasting responses. In another common used procedure, the Fixed Interval schedule (FI), a response will be reinforced if a fixed interval of time has elapsed since the preceding reinforcer delivery. Responses emitted during this interval have no programmed consequences. Temporal regulation of behavior is not required by the FI schedule but develops spontaneously as a consequence of training: each reinforcer is followed by a pause without operant activity, which resumes only towards the end of the interval.

Dependent variables, i.e., temporal estimates collected with these schedules (IRTs in DRL, response durations in DRRD, or post-reinforcement pause durations in FI) can be described by their central tendency (the mean IRT or post-reinforcement pause, for instance) and dispersion indices (such as the standard deviation of IRTs or response durations). Central tendency indices inform us about the accuracy of time estimation; dispersion indices about the sensitivity to differences in time (as does the Weber index in duration discrimination tasks). Both indices thus reflect different aspects of the sensitivity to time. The ratio between the dispersion and the central tendency indices can also be computed. This coefficient of variation gives information about the evolution of the sensitivity to time when the duration to be evaluated changes. The coefficient of variation is considered as equivalent to the Weber fraction computed in duration discrimination tasks. Thus, a constant coefficient of variation suggests that Weber's law not only governs duration discrimination, but also response timing. This last proposal is at the core of scalar timing theory (Gibbon, 1977). Response rate functions in FI can also be considered as analogous to distributions of IRTs or response durations, and treated as such (Lejeune & Wearden, 1991).

Using such procedures, three experimental strategies can be followed to test the above described hypotheses: comparing closely related

species, species without evolutionary connections and, finally, performance obtained in the same species and the same task with different operant responses (Richelle et al., 1985). Comparing humans and turtles does not make sense if the aim is to reconstruct the evolution or "history" of timing abilities, because the two species have no evolutionary connection. Nevertheless, such comparisons gain significance within the anagenetic perspective in comparative psychology. This position bypasses phyletic connections and defines anagenetic grades as levels in a series of ascending improvements on scales of behavioral flexibility or independence with regard to ecological constraints. Defining anagenetic grades is, of course, no easy task. However, the experimental strategies suggested to reach this goal are strikingly similar to those just described: the comparison of similar and different species, the manipulation of the ecological environment of the species, and submitting species to tasks different from those encountered in the natural environment (Gottlieb, 1984). Although criticized as value-laden and confounding increased complexity, progression and progress (Campbell & Hodos, 1991), a comparative psychology based on anagenetic grades is as legitimate as a classification according to phylogeny. It concerns the adaptation of the organism to its environment and thus is related to the ethological hypothesis mentioned above.

As an example of anagenetic comparisons, Figure 1 presents the coefficients of variation collected with the FI, DRL and duration production schedules in seven different species, ranging from fresh water turtles to human subjects. Such crude and limited data cannot be exhibited as a model of comparative research, however, limited as it is, this set of data highlights two main points. Firstly, sensitivity to time is not equivalent in all species: fish and turtles seem to be less sensitive to time than, for instance, cats, albino rats or humans. Usually, coefficients are equal or greater than about .25 in animals, whereas they are around .10 in human subjects. Secondly, in some cases, the coefficient of variation tends to remain roughly constant with changes in the duration timed (in agreement with scalar timing theory) whereas it increases in other cases when the target duration increases. Other data also show that performance depends on biological constraints such as the nature of the operant. In the DRL or DRRD schedules, performance accuracy of pigeons pecking a key breaks down if target durations exceed 20 to 30 seconds or so, whereas precise and stable temporally-regulated behavior can be collected up to 50 or even 70

seconds if a perch-hopping response is used (Jasselette, Lejeune & Wearden, 1990).

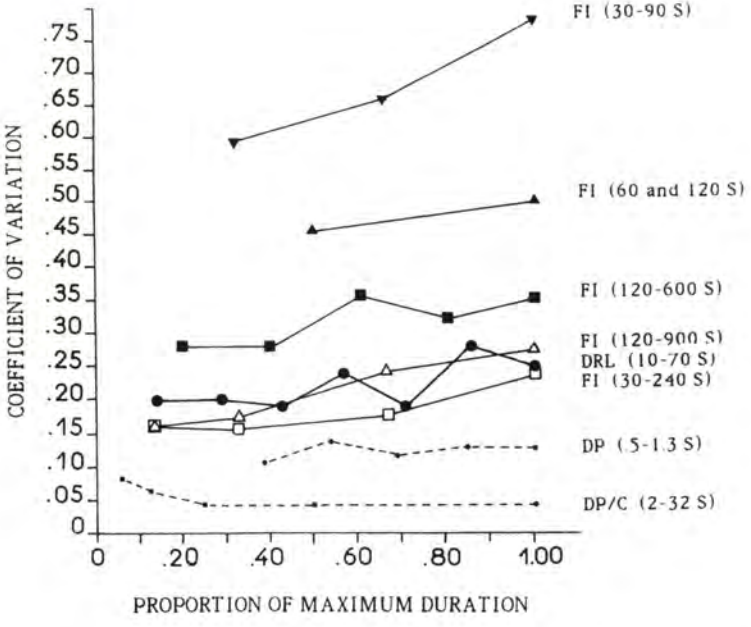


*Figure 1.* Coefficients of variation (ordinate) derived from performance on FI, DRL and duration production (DP) schedules. Target duration (in seconds, abscissa) is expressed as the proportion of the maximum duration investigated. Schedules (FI, DRL and DP) and duration ranges are given to the right of each graph. From top to bottom: ▼: fresh water turtle (*Pseudemys scripta elegans, Wied*); ▲: fish (*Tilapia niloticus* L.); ■: albino rat; Δ : cat; ●: pigeon; ❑: wood mice (*Apodemus sylvaticus*); • and broken lines: human subjects. DP/C indicates duration production with chronometric counting (adapted and modified from Lejeune and Wearden, 1991).

Scalar timing theory can accommodate different levels of sensitivity to time, and thus between-species differences, provided that the coefficient of variation of performance remains constant as the duration timed changes. Cases where the coefficient of variation increases progressively when target time increases are, at first sight, at odds with scalar timing theory and suggest that another mechanism is at work. Nevertheless, this particular trend can also be reconciled with scalar timing, provided that a process generating responses at random is combined with the scalar timer itself. Such random responding

might be triggered, for instance, by the physical characteristics (shape, hue, intensity etc.) of a stimulus conveying the target duration, because these characteristics are predictive of a future reinforcement opportunity, as is the duration of the stimulus (Roberts & Gharib, 1991). Computer simulation of a model combining a scalar timer and a random responding process produced simulated performance compatible with real data (Lejeune & Wearden, 1991). Inter-species differences might thus be understood as deriving from the interaction of a core aptitude similar for all and "peripheral" modulators (as, for example, the just mentioned hypothetical random responding process) which depend on various factors linked to evolution. It thus makes sense to speak about a dissociation between aptitude and performance. However, if scalar timing theory allows for the adaptation of Weber's law to response timing, its generality across species, duration ranges and ages has yet to be demonstrated. Scalar timing has so far been tested only with adult rats, pigeons or humans, and, in most cases, for target durations ranging from about 1 to 60 seconds.

## ANIMAL AND HUMAN: SAME OR DIFFERENT?

Even if quantitative (level of sensitivity) and qualitative differences (increase of the coefficient of variation) are compatible with scalar timing, this does not exclude the possibility that other processes exist. Indeed, the coefficient of variation derived from duration production with counting does not remain constant or increase when the target duration increases, as can be seen of Figure 1. It first decreases before reaching a very low and stable level, at least up to a target duration of 32 seconds.

The main question thus is: how far can behavioral principles valid for animal timing be generalized to the human species and vice versa? Recent publications defend two positions, both relying on analog experiments in animal and human subjects. The first advocates developing human models of animal behavior to extend and test the generality of hypotheses derived from human data. This experimental strategy seemingly violates the principle of economy (Morgan's cannon). Instead of "reducing" human to animal abilities (which does not suppose a negative judgment of value), it rather tends to endow animals with human-like abilities. Differences between humans and animals are not negated, but they are conceived as mostly quanti-

tative and not qualitative (Church, 1993). The second position aims at testing the generalizability of data and theory from animal experiments to issues in human timing research, and suggests that language may offer a clue to timing mechanisms qualitatively different from those found in animals (Wearden & Lejeune, 1993). Strong generalizability supposes that processes at work in humans can be reduced to processes underlying analog animal performances. For example, duration production without counting yields similar data in pigeons and man, in the sense that both sets of data match the predictions of scalar timing theory. Partial generalizability is found when data in humans can be partially explained by processes at work in animals, other controlling processes being unique to the human species. For example, differences between the shape of the temporal generalization gradients described in rats and humans might reflect small differences in the time comparison process applied by the subjects (Wearden, 1992). Finally, weak generalizability concerns cases where animal psychology is useful for understanding human data only by analogy, without postulating a common timing mechanism.

## TIMING WITH LANGUAGE: ANOTHER WORLD?

The above-mentioned examples share a common feature: human experiments were conducted with durations too short (under or around the second) to make verbal time-mediating strategies useful to subjects. They show that, even without words, animal-human generalizability is not always found. The involvement of language may mask animal-like processes or replaced them by different mechanisms, as counting-based duration production seems to show.

Facts offer a less clear picture than expected. The case of the FI schedule is particularly interesting in this respect. Trained animals on FI develop the typical pause-response pattern, with the duration of the pause roughly proportional to the duration of the interval. Adult humans do not. They produce either a high- or a low-rate response pattern, with one or just a few responses at the very end of the interval. The high rate pattern is insensitive to the duration of the interval, whereas the low rate pattern exhibits sensitivity. Without specific instructions about the contingencies at work, adult humans follow self-generated rules. Their performance seems to be verbally controlled or "rule-governed", as opposed to contingency shaped animal behavior.

Do these results mean that animal-like FI patterns cannot be obtained in adult human subjects and that we face here a case where radically different timing processes are at work? It first appeared that following animal-fair procedures with adult humans did not suppress species-related differences (Matthews, Shimoff, Catania & Sagvolden, 1977). However, other attempts have been more successful. Animal-like FI performance could be recorded with an observing contingency added to the operant response, and in infant subjects. In the first case, human adults were instructed to press on a response panel for points to be exchanged for money after the end of the session. Each response briefly lit the display of a digital clock giving in minutes and seconds the time elapsed since the last reinforcer delivery. A pause-response pattern developed, which was sensitive to the duration of the FI, as is the case for pigeons or rats. Providing a response-dependent clock thus induced an interval-based description of the contingency and avoided the need for self-produced interpretations or response rules (Lowe, 1979). In the second case, animal-like performances were produced by infants aged about 10 months, i.e., an age when control of behavior by verbal response rules is highly improbable. Sensitivity to schedule parameters was obtained with several FI values, ranging from 10 to 50 seconds (Lowe, Beasty & Bentall, 1983). It follows from such data that before the mastery of language, animal-like biological processes might be at play. According to Bentall, Lowe and Beasty (1985), language is the main variable responsible for animal-human differences in FI.

However, this interpretation of the role of language has recently been called into question by other sets of data. Firstly, the transition from animal-like to typically adult FI responding is progressive and does not exactly match the development of verbal competence. In particular, adult-like performance appears only from 5 or 6 years on, long after basic verbal skills have been acquired (Pouthas & Jacquet, 1985). A dissociation between saying and doing has also been observed in children during a duration production task (Pouthas, Droit, Jacquet & Wearden, 1990), suggesting that the relationship between timing and language is much more complicated than first thought.

Secondly, adult-like low rate responding has been described in infants aged from 3 to 5 months. Furthermore, infants aged 9 to 13 month (the same age as those from Lowe et al., 1983) produced either high- or low-rate response patterns, similar to those reported from adults (Darcheville, Rivière & Wearden, 1993). All low-rate subjects

produced mean post-reinforcement pauses matching the duration of fixed intervals ranging from 10 to 80 seconds. These data invalidate the claim of strong generalizability from animal to human infants and suggest that language does not explain the differences between humans and animals. Timing without language, at least in FI, is not necessarily similar to animal timing.

Finally, human-like FI behavior has been obtained in animals, as a consequence of the training procedure. Low-rate FI responding was recorded in adult albino rats on an around-the-clock multiple FI-extinction schedule, where 30-minute FI 60 seconds sessions alternated with 90-minute rest periods. Comparison with human adults using chronometric counting in the same FI revealed no striking differences in response pattern or rates (less than 1 per minute), but the characteristic species-related difference in sensitivity to time: the coefficient of variation of the distribution of pause durations was .11 in humans, and .25 in rats (Lejeune & Richelle, 1990). Limited as they are, these data however show that rats need only intensive training to perform in the same way as human adults using a time-related response rule in FI.

## Conclusions

Is the comparative psychology of timing worth studying? The answer to this question depends on the weight or importance given to human abilities with regard to those typical of animal subjects. For those exclusively fascinated by human performance, comparative psychology of timing may appear as wasteful or old-fashioned. However, gaining insight into the specificity of human timing aptitude cannot be achieved without cross-species comparisons taking also the developmental dimension into account. Admitting that language may influence timing abilities does not imply that humans are radically different from other species and does not negate Darwinian between-species continuity.

If between-species comparisons are accepted as interesting, three decisions must be taken: which species to compare, which aim to follow and which procedures to adopt. As argued above, a comparative psychology of timing within an anagenetical perspective does not require the selection of species on the basis of clearcut phyletic criteria. The description of species-specific timing processes is of course the

ultimate goal of a comparative psychology of time. It might nevertheless be regretted that publications dealing with timing mechanisms rarely take the comparative dimension into account. In other respects, methodology is not independent from the model under investigation. If the timer is conceived as some core mechanism whose expression can be biased by "peripheral" variables, whatever they might be, investigators will design or select procedures best suited to unveil timing untainted by such interfering variables. The peak procedure, which derives from FI, is at present the most favored methodological tool in the domain of response timing. It is premature to say if favoring this procedure while neglecting some others was a good choice.

It goes without saying that aspects of human timing relying on language, such as the reasoning or metaphors on time, cannot be investigated with animal subjects. Although several analog temporal discrimination or regulation procedures have been designed, two domains pose special difficulties. Retrospective timing (the verbal estimation of a single elapsed duration sample, without previous warning about the future task) and responding synchronously with a regular beat have not yet been adapted for animal subjects. However, advances in methodology have progressively revealed that animal timing is much more sophisticated than first thought. Animals are able not only to produce, reproduce or compare durations, they can also deal with duration scales and relative duration ratios (Dreyfus, 1992). Studies on the memory and representation of time may even be more advanced in animals than in humans (Spetch & Ruzak, 1992). Development of knowledge in related fields, such as foraging, further reinforce the image of a temporally competent animal (Krebs & Kacelnik, 1984).

In summary, even if similar forms of adjustment could be described in animal and human subjects, it would be premature to promote a view according to which the inter-species generality issue is settled (Lejeune, 1990). Strong generalizability from animal to human data is limited to particular species (pigeons and rats) and experimental settings. Focussing research exclusively on such cases may hamper concern about exceptions. Several questions remain outstanding today, and they cannot be answered without investigating more species and maintaining a dialogue between designing models and collecting facts which are truly representative of the diversity of adaptations to time.

## REFERENCES

Bentall, R. P., Lowe, C. F., & Beasty, A. (1985). The role of verbal behavior in human learning: II Developmental differences. *Journal of the Experimental Analysis of Behavior, 43*, 165-181.

Campbell, C. B. G., & Hodos, W. (1991). The scala naturae revisited: Evolutionary scales and anagenesis in comparative psychology. *Journal of Comparative Psychology, 105*, 211-221.

Catania, A. C. (1970). Reinforcement schedules and psychophysical judgment: a study of some properties of behavior. In W. N. Schoenfeld (Ed.), *The theory of reinforcement schedules* (pp. 1-42). New York: Appleton Century Crofts.

Church, R. M. (1984). Properties of the internal clock. In J. Gibbon & L. Allan (Eds.), *Timing and time perception* (pp. 566-582). New York: Annals of the New York Academy of Sciences, 423.

Church, R. M. (1993). Human models of animal behavior. *Psychological Science, 4*, 170-173.

Darcheville, J. C., Rivière, V., & Wearden, J. (1993). Fixed interval performance and self-control in infants. *Journal of the Experimental Analysis of Behavior, 60*, 239-254.

Dreyfus, L. R. (1992). Absolute and relational control in a temporal comparison task. In W. K. Honig & J. G. Fetterman (Eds.), Cognitive aspects of stimulus control (pp. 21-46). Hillsdale, NJ: Lawrence Erlbaum.

Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychological Review, 84*, 279-325.

Gottlieb, G. (1984). Evolutionary trends and evolutionary origins: Relevance to theory in comparative psychology. *Psychological Review, 91*, 448-456.

Jasselette, P., Lejeune, H., & Wearden, J. (1990). The perching response and the laws of animal timing. *Journal of Experimental Psychology: Animal Behavior Processes, 16*, 150-161.

Krebs, J. R., & Kacelnik, A. (1984). Time horizons and foraging animals. In J. Gibbon & L. Allan (Eds.), *Timing and time perception* (pp. 278-291). New York: Annals of the New York Academy of Sciences, 423.

Lejeune, H. (1990). Timing: Differences in continuity or generality beyond differences? In D. Blackman & H. Lejeune (Eds.), *Behaviour analysis in theory and practice: Contributions and controversies* (pp. 53-90). London: Lawrence Erlbaum.

Lejeune, H., & Richelle, M. (1990). Timing behavior and development: Comments on some animal and human data. *International Journal of Comparative Psychology, 4*, 111-135.

Lejeune, H., & Wearden, J. (1991). The comparative psychology of fixed interval responding: Some quantitative analyses. *Learning and Motivation, 22*, 84-111.

Lowe, C. F. (1979). Determinants of human operant behaviour. In M. D. Zeiler & P. Harzem (Eds.), *Advances in the analysis of behaviour: Vol. 1. Reinforcement and the organization of behaviour* (pp. 159-192). Chichester: Wiley.

Lowe, C. F., Beasty, A., & Bentall, R. P. (1983). The role of verbal behavior in human learning: infant performance on fixed interval schedules. *Journal of the Experimental Analysis of Behavior, 39*, 157-164.

Matthews, B. A., Shimoff, E., Catania, A. C., & Sagvolden, T. (1977). Uninstructed human responding: Sensitivity to ratio and interval contingencies. *Journal of the Experimental Analysis of Behavior, 27*, 453-467.

Platt, J. R. (1979). Temporal differentiation and the psychophysics of time. In M. D. Zeiler & P. Harzem (Eds.), *Advances in the analysis of behaviour, Vol. 1: Reinforcement and the analysis of behaviour* (pp. 1-29). Chichester: Wiley.

Pouthas, V., Droit, S., Jacquet, A. Y., & Wearden, J. (1990). Temporal differentiation of response duration in children of different ages: developmental changes in relations between verbal and nonverbal behavior. *Journal of the Experimental Analysis of Behavior, 53*, 21-31.

Pouthas, V., & Jacquet, A. Y. (1987). A developmental study of timing behavior in 4 1/2- and 7-year-old children. *Journal of Experimental Child Psychology, 43*, 282-299.

Richelle, M., & Lejeune, H. (Eds.)(1980). *Time in animal behaviour*. London: Pergamon Press.

Richelle, M., Lejeune, H., Fery, P., & Perikel, J. J. (1985). From biotemporality to nootemporality: Towards an integrative and comparative view of time in behavior. In J. A. Michon & J. L. Jackson (Eds.), *Time, mind and behavior* (pp. 75-99). Berlin: Springer.

Roberts, S., & Gharib, A. (1991). Peak procedure evidence for a separately changeable dimension-selection process. Poster presented at the 32th Annual Meeting of the Psychonomic Society, San Francisco, California, November 22-24.

Spetch, M. L., & Ruzak, B. (1992). Time present and time past. In W. K. Honig & J. G. Fetterman (Eds.), *Cognitive aspects of stimulus control* (pp. 47-68). Hillsdale, NJ: Lawrence Erlbaum.

Wasserman, E. A. (1993). Comparative cognition: Beginning the second century of the study of animal intelligence. *Psychological Bulletin, 113*, 211-228.

Wearden, J. H. (1991). Do humans possess an internal clock with scalar timing properties? *Learning and Motivation, 22*, 59-83.

Wearden, J. H. (1992). Temporal generalization in humans. *Journal of Experimental Psychology: Animal Behavior Processes, 18*, 134-144.

Wearden, J. H., & Lejeune, H. (1993). Across the great divide: Animal psychology and time in humans. *Time and Society, 2*, 87-106.

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