

Asymmetry of the discrimination function for temporal durations in human subjects

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Abstract. Ten human subjects were comparing durations of pairs of visual stimuli in a two-way forced-choice task. Mean durations of presented time intervals were ~3 s ("short") or ~6 s ("long"); the duration ratio was varied at nine levels. The Weber fractions for the short and long durations were approximately equal, ~0.22. The ratio of subjective equality was almost exactly unity for the short durations, but it was significantly reduced (~0.76) for the long durations. This asymmetry of the discrimination function indicates time-dependent change of internal representations of past durations, and is well compatible with the "dual klepsydra model". Model-based estimates of the internal time representation loss rate, derived from the present data, are in a good agreement with values obtained from earlier studies on duration reproduction.

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INTRODUCTION

Differential sensitivity, that is, the ability to discriminate between stimuli of different magnitudes, is one of basic characteristics of sensory systems, or, more generally, of systems of neural representations of experiential modalities (space, time, numerosity). Among the latter, the time dimension deserves a particular interest for its obviously fundamental role in the organization of behavior and the structure of subjective experience.

Contemporary studies on temporal discrimination have mostly focused on the sub-second domain, i.e., on perception of durations in the order of magnitudes from 10⁻¹ to 10⁰ s (Allan 1977, Getty 1975, Grondin 1993, Hellström 2003, Hellström and Rammsayer However, the subjective experience of an 2004). extension separating distinct events in time fully develops only beyond the horizon of the "extended present," which is usually estimated to 2-3 s (Fraisse 1963, Pöppel 1978, 2004). Data on "time perception" in the supra-second domain (from 10° to 10¹ s and longer) are equally, if not even more, important for our understanding of the intra-organismic representation of temporal durations and, specifically, of the human experience of time (Wackermann et al. 2005, Wackermann 2007 - in press).

Another method to study "time perception" applied preferably in the supra-second domain, is the method of duration reproduction (Woodrow 1951). The relation between a comparison of two subsequent time intervals and a reproduction of a previously perceived interval is obvious: Reproduction can be conceived as an on-going comparison of the second interval to the first one; or, *vice versa*, a comparative judgment can result from a "silent" parallel reproduction of the first interval. Therefore, models of duration reproduction should be applicable to duration discrimination as well.

Of special interest here is the "dual klepsydra" model (DKM) (Wackermann and Ehm 2006, Wackermann et al. 2003). In the model, durations of perceived events are represented by states of inflow/outflow units or "leaky accumulators", acting as integrators of neural excitatory "flows" and losing the accumulated quantity at the rate proportional to the momentary state. The proportionality factor, represented by parameter κ , plays an important role in the theory: its inverse, κ^{-1} , specifies the relaxation time of the hypothetical accumulators. Two such "leaky accu-

mulators" are allocated for parallel representation of two subsequent temporal durations (e.g. in the duration reproduction or discrimination tasks) and their states are continuously compared; two durations are subjectively perceived as equal if the accumulated states are equal. Results of a study by Jech and coauthors (2005), in which the duration reproduction task was combined with the functional magnetic resonance imaging, support the hypothesis of spatially distinct cortical areas differently activated during subsequently perceived time intervals. The DKM accounts naturally for the progressive shortening of reproduced times with increasing duration – an empirical fact challenging other models of time representation – and matches experimental reproduction data with a good accuracy; the resulting estimates of parameter κ are in the order of magnitudes ~10⁻² s⁻¹. Besides the data-based evidence, there are additional theoretical reasons in favor of the DKM-theoretical "klepsydraic reproduction function" as the ideal form of a "law of duration reproduction" (Wackermann 2006).

The aim of the reported study was to examine discriminability of temporal intervals in the supra-second domain for two different classes of durations: just above the "extended present" horizon (average ~3 s) and distinctly longer (average ~6 s). In addition to characterization of the data by the usual psychophysical measures, we attempted an interpretation of the findings in terms of the dual klepsydra model.

METHODS

Subjects

Ten unpaid volunteers (six males, four females, age range 25–61 years, mean age 36.8 years) participated in the study. The participants were informed on the purpose of the study and signed a written consent. All had normal or corrected-to-normal vision, were reportedly of good health, and had no serious neurological or psychiatric problems in their medical records.

Apparatus

A two-way forced-choice duration discrimination task was used. The subjects compared two temporal durations, t_1 and t_2 , marked by appearance of a visual stimulus ("carrier") on a 12" LCD panel of a Pentium III 450 MHz portable computer (Fig. 1a). The carrier

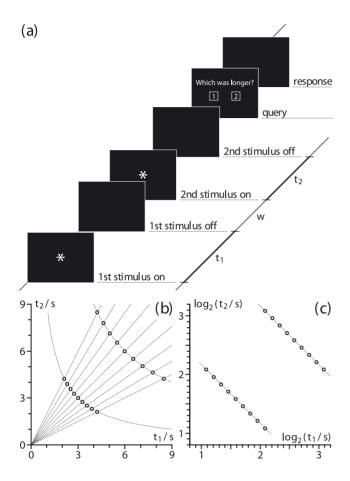


Fig.1. (a) Time chart of the duration discrimination task. (Note: For the sake of legibility, the carrier stimulus and displayed text are magnified and not shown in real proportions to the screen size.) (b) Stimulus durations used in the experiment (scales in seconds). The circles mark pairs of durations (t_1,t_2) belonging to classes S_3 or S_6 (dotted hyperboles), distributed at equal ratios t_2/t_1 (dotted lines). (c) Stimulus durations in log-transformed coordinates (logarithm base 2).

stimulus was a white asterisk of 5 mm diameter (angular size ~40 arc min at the average eye-to-screen distance ~45 cm) shown on a black background; the screen was blank during the inter-stimulus interval, w. After the presentation of the second carrier, the subjects had to indicate which of two durations was longer, choosing one of two displayed response boxes with a pointing device. A neutral response ("apparently equal") was not possible.

Stimuli

The method of constant stimuli was applied. Two sets S_m of duration pairs (t_1, t_2) were defined,

$$m = \sqrt{t_1 t_2} = \text{const}, \ t_2 / t_1 = 2^{k/4} (k = -4, ..., +4)$$
 (1)

with m=3 s ("short") or m=6 s ("long"). In both stimulus classes, S_3 and S_6 , the duration ratios varied, in a geometric sequence, at the same nine levels from 0.5 to 2 (Fig. 1b). The stimuli were thus distributed along two separate linear manifolds in the space of log-transformed durations, with the log-ratio $\lambda = \log_2(t_2/t_1)$ varying from -1 to +1 at equal steps, 0.25 (Fig. 1c).

Experimental procedure

Each subject participated in one experimental session. The sessions consisted of $144 = 2 \times 9 \times 8$ pairwise comparisons: two stimulus classes ("short" vs. "long"), nine duration ratios (see above, Eq. 1), and eight repetitions for each (class, ratio) combination. The stimulus pairs were presented in a randomized order w.r.t. the duration class and ratio. The interstimulus interval between the end of the first and the beginning of the second carrier (Fig. 1a) was constantly w=2 s in all comparisons. The interval from the end of the second carrier to the guery was 1.5 s. There was no fixed inter-trial interval; the subjects had to press a button on the response device to advance to the next trial.

No feedback on the subject's correct or incorrect response was provided during the session. Prior to the experiment, the subjects were verbally discouraged from sub-vocal "mental counting" or similar timekeeping strategies (e.g. hand or foot tapping). There were no additional controls as to whether the subjects refrained from counting.

Data reduction and analysis

Subjects' responses were sorted by the duration ratios and classes, and relative frequencies of the response 2 = "2nd duration perceived as longer" were calculated separately for each subject and stimulus Psychometric functions (PMF) (Luce and Galanter 1963) of the log-ratio λ ,

$$\Psi(\lambda) \equiv \Pr\left(2\left|\log(t_2/t_1)\right) = \lambda\right) = \Phi\left(c\frac{\lambda - \theta}{\omega}\right)$$
 (2)

were fitted to the data. In Eq. 2, $\Phi(.)$ denotes the normal (Gaussian) cumulative distribution function,

¹ These terms are used in the present paper only in the relative meaning, i.e., to distinguish between two classes of stimuli. In the nomenclature of modern studies on "time perception", a duration 1000 ms is usually considered as being "long".

 θ is the "point of subjective equality", ω is an inverse measure of discrimination sensitivity, and $c = \Phi^{-1}(\frac{3}{4}) \approx 0.6745$ is a constant chosen so that a difference of 1 ω is the "just noticeable difference". The parameters θ and ω were estimated by the maximum-likelihood method (Bush 1963)².

According to the definition, θ is the value of the relevant stimulus property, λ , for which the probabilities of perceiving the first or the second duration as "longer" are equal, i.e., $\frac{1}{2}$; hence "point of subjective equality" (PSE). The stimulus variable, λ , is defined on a logarithmic scale, so that the zero point corresponds to physical equality of both durations, $t_2/t_1=1$, that is, $t_2=t_1$. The "just noticeable difference" (JND) is, by convention (Guilford 1931), a difference from the PSE for which the probability of response "2nd duration perceived as longer" changes to $\frac{3}{4}$ vs. $\frac{1}{4}$ (a probabilistic re-definition of the concept of "differential threshold"; cf. Gescheider 1997, pp. 50–54).

The PSE and JND were the parameters of our prime interest. Within-sample differences of estimated PSEs from 0, or intra-individual differences between PSEs or JNDs for different stimulus classes, were assessed by the Wilcoxon's symmetry test (Lentner 1982). In addition, two descriptive parameters, the "ratio of subjective equality" (RSE) and the "Weber fraction" (WF) were calculated from PSEs and JNDs.

For a given stimulus class, S_m , and PSE estimate, θ , the subjectively equal durations are

$$t_1^{\text{o}} = m e^{-\frac{1}{2}\hat{\theta} \ln 2}, \ t_2^{\text{o}} = m e^{+\frac{1}{2}\hat{\theta} \ln 2}$$
 (3)

and the ratio of subjective equality (RSE) is thus

$$\frac{t_1^{\text{o}}}{t_2^{\text{o}}} = e^{\widehat{\theta} \ln 2} \tag{4}$$

The Weber fraction (WF) is a relative, dimensionless measure of differential sensitivity. The WF is traditionally defined as the ratio $\Delta s/s$, where Δs is the "just noticeable" change of stimulus and s is the actual stimulus magnitude. In our design there is no "standard" stimulus, s, since both members of the stimulus pair are varied in the stimulus manifolds S_3 and S_6 . In accord with the traditional definition, we define the Weber fraction via the symmetrical difference of two JNDs, $s-\Delta s$ and $s+\Delta s$, which leads to a formula

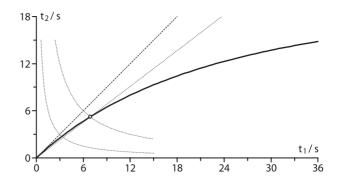


Fig. 2. Example of the reproduction function matching procedure. The ray $t_2/t_1 = \text{RSE}$ (dotted line) intersects the stimulus manifold $\sqrt{t_1t_2} = 6$ s (upper dotted hyperbole) in a point (t_1^o, t_2^o) (marked by circle) through which the reproduction function is drawn (thick solid curve). The entire curve is located below the line $\{t_2 = t_1\}$ (dashed line) that corresponds to the exact reproduction or to a symmetrical discrimination function, respectively.

$$WF = \tanh (\omega \ln 2) \tag{5}$$

Finally, of interest were values of the DKM parameter, κ , matching subjectively equal durations (t_1^0, t_2^0) . The model yields a "klepsydraic reproduction function",

$$r(s, w) = \kappa^{-1} \ln(1 + \eta (1 - e^{-\kappa s}) e^{-\kappa w})$$
 (6)

where s is the duration of a presented time interval, w is the inter-stimulus interval (which was constant in the present study), and r is the duration of the reproduced interval. By simple algebraic manipulations, Eq. 6 is transformed to the form

$$\frac{e^{\kappa(s+w+r)} - e^{\kappa(s+w)}}{e^{\kappa s} - 1} = \eta \tag{7}$$

where the two parameters, κ and η , are separated.³ The parameter η represents the ratio of internal excitatory flows caused by the carrier stimuli (see Introduction). If identical carriers are used to mark both temporal intervals, as in our experiment, η =1 is a plausible assumption (Wackermann and Ehm 2006, p. 486). Eq. 7 with fixed η =1 thus becomes an equation in a single variable, κ , which has a unique solution $\kappa \ge 0$ for any $s \ge r$. Substituting $t_1^o \to s$, $t_2^o \to r$ and solving Eq. 7 by an iterative numerical procedure,⁴ we obtained estimates $\hat{\kappa}$ for the PSEs in the stimulus manifold S_6 , as illustrated in Fig. 2.

² In the following text a superscripted caret, ^, indicates a data-based estimate of a parameter.

³ The limiting value of the lh.s. in Eq. 7 for $\kappa \to 0$ is r/s.

⁴ An approximate solution of Eq. 7 with $\eta = 1$ for small values of κ is $\kappa = \frac{2(s-r)}{(s+\omega+r)^2-(s+\omega)^2-s^2}$

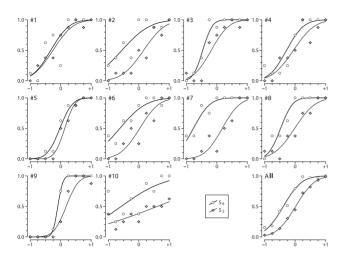


Fig. 3. Response data and fitted psychometric functions for the individual subjects, and averaged across subjects #1-#9 ("All"). Abscissae: logarithm (base 2) of the duration ratio, 2nd vs. 1st carrier; $0 = point of physical equality, <math>t_1 = t_2$. Ordinates: relative frequency or probability of response 2 ("2nd duration perceived as longer"). Rhomboid markers/thin curves: stimulus class S_3 ("short" durations); circular markers/thick curves: stimulus class S_6 ("long" durations).

RESULTS

Individual response frequencies and fitted PMFs (Fig. 3) show a considerable inter-individual variability of the PMFs in terms of their positions and slopes. The same is true for the PMFs for the "short" and "long" durations compared intra-individually: in some cases (e.g. #7), the PMFs are merely shifted along the λ-axis; in other cases the slopes clearly differ (e.g. #3 and #9). An extremely high percentage of errors and a poor fit of the PMFs to the data in the subject #10 indicate that she probably failed to follow the instruction. Therefore, the subject #10 has been excluded from further analyses; in the following, "all" refers to nine remaining subjects (six males, three females, mean age 38.1 years).

The individual estimates of PMF parameters and derived parameters are summarized in Table I, along with their arithmetic means across all subjects. The values printed in the row labeled "All" were obtained by fitting PMFs to the relative frequencies averaged across all subjects.5

Table I Parameters of psychometric functions and derived parameters for the individual subjects and for aggregated data

Subject	Stimulus class S ₃ ("short")				\$	Stimulus class S ₆ ("long")			
	PSE	JND	RSE	WF	PSE	JND	RSE	WF	
1	-0.254	0.353	0.839	0.240	-0.325	5 0.323	0.798	0.220	
2	0.158	0.375	1.116	0.254	-0.553	0.492	0.682	0.328	
3	-0.184	0.308	0.880	0.210	-0.46	0.167	0.726	0.115	
4	-0.054	0.371	0.963	0.252	-0.28î	0.301	0.823	0.205	
5	0.132	0.176	1.096	0.121	-0.028	0.219	0.981	0.151	
6	0.030	0.340	1.021	0.231	-0.621	0.462	0.650	0.309	
7	0.178	0.308	1.131	0.210	-0.770	0.294	0.586	0.201	
8	-0.015	0.360	0.990	0.244	-0.475	0.211	0.719	0.145	
9	0.180	0.217	1.133	0.149	-0.094	1 0.088	0.937	0.061	
10*	0.605	1.382	1.521	0.743	-0.578	0.756	0.670	0.481	
Mean†	0.019	0.312	1.013	0.213	-0.40	0.284	0.757	0.194	
All	0.016	0.330	1.011	0.225	-0.388	3 0.324	0.764	0.221	

Abbreviations: (PSE) point of subjective equality; (JND) just noticeable difference; (RSE) ratio of subjective equality; (WF) Weber fraction. Notes: * Not included in calculations of "Mean" and "All" parameters. † Entries printed in slanted typeface are not group averages: these values were calculated from mean PSEs and JNDs, using Eqs 4 and 5.

⁵ The minor differences between the "Mean" and "All" rows of Table I are naturally due to the non-linear form of the PMF, so that the operations of averaging and estimating PMF parameters do not commute. Generally, the "All" estimates are to be considered as more robust.

The PSEs for the S_3 class are roughly symmetrically scattered around zero (Wilcoxon's one-sample test, T_- =24, ns, whereas the PSEs for the S_6 class are all negative (Wilcoxon's one-sample test, T_- =0, P<0.002). In all subjects the PSEs for S_6 are consistently smaller than the PSEs for S_3 (Wilcoxon's matched-pairs test, T_- =0, P<0.002). This effect is clearly visible in Fig. 3 (section "All"), where the PMFs for the S_6 class are shifted to the left from the PMFs for the S_3 class.

The JNDs for the two classes of stimuli are of comparable magnitudes. The JNDs for the long durations (S_6) are, on the average, only slightly smaller than the JNDs for the short durations (S_3) ; the difference is not significant (Wilcoxon's matched-pairs test, $T_-=4$, ns). There is no apparent relation between individual PMF parameters and the subjects' age (Spearman's rank correlations: all $|\rho| < 0.4$, ns). Individual PSEs for the short and long durations are also unrelated (Spearman's $\rho = -0.117$, ns), but there is a moderate positive intra-individual correlation between JNDs determined for the "short" and "long" durations (Spearman's $\rho = +0.65$, $P \approx 0.06$).

Table II

Pairs of subjectively equal durations (t_1^0, t_2^0) in the stimulus manifold S_6 , and values of the parameter κ of matching reproduction functions

Subject	$t_1^{\rm o}$ [s]	$t_2^{\rm o}$ [s]	$\hat{\kappa}$ [s ⁻¹]
1	6.716	5.360	0.0281
2	7.267	4.954	0.0476
3	7.041	5.113	0.0398
4	6.614	5.443	0.0243
5	6.058	5.943	0.0024
6	7.440	4.839	0.0533
7	7.836	4.594	0.0659
8	7.075	5.088	0.0410
9	6.199	5.807	0.0082
10*	7.331	4.911	0.0497
Mean†	6.895	5.221	0.0346
All	6.863	5.246	0.0335

Notes: * Not included in calculations of "Mean" and "All" parameters. † Entries printed in slanted typeface are not group averages: these values were calculated from the mean PSE, using Eqs 3 and 7.

The parameters of reproduction functions matching RSEs are given in Table II. The individual estimates $\hat{\kappa}$ are in the range from 2.4×10^{-3} to 6.6×10^{-2} s⁻¹. The estimate from the PSE determined for the entire sample PMF is $\hat{\kappa}$ =0.033 s⁻¹; the difference from the sample mean is negligible.

DISCUSSION

Sensitivity: Weber fractions

The Weber fractions (WF) for both stimulus classes, S_3 and S_6 , are, on the average, ~ 0.22 . This is a relatively high value, compared to the WFs obtained for duration discrimination by other authors. However, comparisons against values reported in the literature should be taken with caution, since the discrimination performance may depend on a number of instrumental factors, such as the sensory modality of duration markers or carriers (Goodfellow 1934) and/or the presentation mode (for a review see Grondin 2001): WFs for durations delimited by auditory stimuli are lower than for visual stimuli, and slightly lower for "empty" time intervals than for "filled" intervals, at least in the sub-second region (Grondin Nonetheless, the WF value for visually marked "filled" duration ~3 s (interpolated from Fig. 2 in Grondin 2003, p. 37) is about 0.045, that is by factor 5 smaller than ours.

Degree of practice in the task, and feedback may also play a considerable role (Allan and Kristofferson 1974, Woodrow 1935). In our study, subjects had no pre-experiment training, and no feedback was provided during the experimental session. These conditions best suit our aim to explore duration discrimination in its "native" form; however, comparisons against studies in which subjects were trained to their optimum performance would be misleading. As noted by Hellström and Rammsayer (2004, p. 18), "[...] the practice of providing feedback has beneficial effects in that it reduces inter-individual variability; however, it may also have fundamental effects on the comparison process and, therefore, on discrimination performance."

It is well known that the WF does not remain constant across larger ranges of durations (Grondin 2001, 2003).⁷ The dependence of the WF on the reference magnitude is well explored for very short durations, whereas the supra-second domain has been less intensely explored. An early study by Quasebarth

⁶ Correlations for the derived parameters (i.e., the ratio of subjective equality and Weber fraction) are not mentioned, because these parameters are obtained from the primary PMF parameters (Eqs 4 and 5) and Spearman's rank correlation is invariant under monotonic data transformations.

This is often referred to as a "violation of Weber's law". However, the WF is a useful characteristic of discriminability within a certain region of stimulus magnitudes, regardless if the "law" holds good for larger ranges of magnitudes or not.

(1924), using continuous light stimuli of durations from 2 to 8 s, reported WFs from 0.07 to 0.14. Later, Getty (1975) studied discrimination of empty, auditorily marked intervals and found a gradual increase of WFs for "standard" durations ≥2.5 s, reaching values of ~0.15. These values are still by factor 1.5–3 smaller than those obtained in our study. However, Droit-Volet and Wearden (2001) reported WFs comparable with ours, ≥ 0.2 , for durations 1–4 and 2–8 s in a group of 8-years old children. More research focusing specifically on the supra-second domain may be needed to obtain really representative values. With all these reservations we conclude that the Weber fraction for duration discrimination in the domain of our interest, 3 to 6 s, in naive subjects without prior training, is approximately $\frac{1}{4}$ to $\frac{1}{5}$. We cannot claim, however, that duration discrimination in the supra-second domain is strictly Weberian.8

Subjective equality: "time-order error"?

The most robust result from the present study is the systematic negative shift of the PSEs for long durations (\sim 6 s), observed in all subjects. RSE≈0.76, the subjective equality corresponds to physical inequality of durations, where the latter duration is about $\frac{3}{4}$ of the former. This outcome, reminding of a so-called "time-order error" or "presentation order effect," requires an interpretation.9

The "time-order error" was discovered by Fechner (1860, section VIII.1c) in experiments with muscular effort sensations: in a comparison of two subsequently lifted weights, the latter was judged as relatively heavier. Since then the effect has been found for many sensory modalities and experiential continua, including perception of temporal durations (e.g. Allan 1977, Hellström 2003, Hellström and Rammsayer 2004, Jamieson and Petrusic 1975, Stott 1935), and elicited a plenitude of theoretical explanations. scope of the present paper does not allow an extensive review (see e.g. Hellström 1985); the discussion will be thus limited to a few comments relevant to our results.

The notion of "time-order error" originates from a special variant of the method of constant stimuli (Fechner 1860, Gescheider 1997), in which a variable

tion of the error should be explained by a relevant psychological theory.

stimulus, v, is compared to a constant stimulus, s (also called "standard"). The PMF is considered as a univariate function of v. It is found that, depending on whether the "standard" precedes or follows the variable stimulus, the PSEs determined by this method are generally different. In a somewhat sloppy phrasing, "the order of comparison matters", which may invoke psychological explanations in terms of "attention allocation" or "response bias".10

In fact, the "time-order error" is a particular manifestation of the form of the discrimination function.

$$\Upsilon(x_1, x_2) \equiv \Pr(\mathbf{2}|x_1, x_2)$$
 (8)

that is, a bivariate function assigning probability of response 2 to a pair of stimuli of magnitudes $x_1, x_2,$ compared in this order. Applying the method of constant stimuli with a fixed standard, s, two PMFs are constructed,

$$\Psi_1(v) = \Upsilon(s, v), \ \Psi_2(v) = 1 - \Upsilon(v, s)$$
 (9)

for which their respective PSEs are determined, θ_i , such that $\Psi_i(\theta_i) = \frac{1}{2}$ (i=1: standard precedes, i=2, standard follows). These PMFs are two partial (univariate) functions obtained by "cutting" the bivariate discrimination function Y in two directions, i.e., along two deliberately chosen one-parametric stimulus manifolds (Fig. 4).

If the function Υ were exactly anti-symmetrical,

$$\Upsilon(x_1, x_2) + \Upsilon(x_2, x_1) = 1$$
 (10)

then the manifold of subjectively equal stimulus pairs

$$\mathbf{E} = \{ (x_1, x_2) | \Upsilon(x_1, x_2) = \frac{1}{2} \}$$
 (11)

would be identical to the manifold of physically equal stimulus pairs (identity),

$$I = \{(x_1, x_2) | x_1 = x_2\}$$
(12)

and $\theta_1 = \theta_2$ would hold good (Fig. 4a). If, for whatever cause, the discrimination function is shaped so

⁸ Incidentally, the relatively low differential sensitivity indicates that the subjects were very probably not using auxiliary techniques such as "mental counting". 9 Interestingly, no significant deviation of the PSE from zero is seen for short durations (~3 s), and there is no apparent intra-individual correlation between PSEs obtained for short and longer durations. This may indicate that different mechanisms are underlying discrimination of short durations, below or at the horizon of the "extended present" (cf. Introduction). The following interpretation applies exclusively to long durations showing a distinct asymmetry of the discrimination function. 10 There may be a semantic ambiguity contributing to conceptual problems of the "time-order error" interpretation: In a physicist's language (Fechner), an "error" is a term additively superimposed on the quantity which is the object of the measurement. Hence, "constant error" ("konstanter Fehler") is merely a name for a systematic deviation, i.e., an error term of a non-zero expectancy; the same applies to the so-called "time error" ("Zeitfehler") that was by Fechner conceived as a component of the systematic (constant) error. In a psychologist's understanding, however, "errors" are actively produced by the cognizing subjects, and it is felt that the produc-

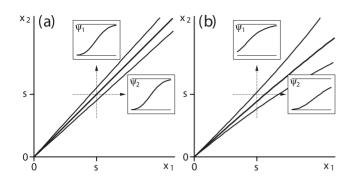


Fig. 4. Univariate PMFs obtained by "cutting" the bivariate discrimination function Υ in two orthogonal directions (dotted arrows). The curves indicate manifolds of equal probability $\Pr(2 \mid x_1, x_2) = p$ for $p \in \{\frac{1}{4}, \frac{1}{2}, \frac{3}{4}\}$ (the thick line/curve correspond to $p = \frac{1}{2}$, i.e., to the manifolds of subjectively equal stimuli, E). The forms of resulting PMFs Ψ_1 , Ψ_2 , are shown in the inserted boxes. (a) Exactly anti-symmetrical discrimination function: $\Psi_1 = \Psi_2$; (b) deviation from antisymmetry: $\Psi_1 \neq \Psi_2$.

that E deviates from I, the two PMFs necessarily differ, and so their respective PSEs are different: $\theta_1 \neq \theta_2$ (Fig. 4b). The observed difference is then a consequence of a particular method of sampling the space of stimulus pairings $\{(x_1, x_2)\}$, rather than a simple measurement "error."

Of interest is the form of the entire manifold E in the two-dimensional space of possible stimulus pair-A single-value determination of the PSE is meaningful only for a properly defined and parameterized stimulus manifold S, so that the point of intersection $S \cap E$ is uniquely localized. The choice of the manifold S is a matter of the experimenter's decision: the "fixed standard" strategies are by no means privileged (except of the ease of physical realization) and, in fact, suboptimal w.r.t. the objectives of the experiment. Ideally, differential sensitivity should be measured in the direction of the gradient of the discrimination function Υ at a given PSE, to ensure the maximal steepness of the PMF. In a case of insufficient or no prior knowledge of the function Υ , a convenient choice is to make the stimulus manifold Sorthogonal to the manifold I, assuming that E does not deviate from *I* too largely.

In our experiment, the stimulus classes S_3 and S_6 , defined by Eq. 1, were subsets of stimulus manifolds which were locally orthogonal to the line $\{t_1 = t_2\}$ and parameterized by the log-ratio $\lambda = \log_2(t_2/t_1)$ (Fig. 1c). The estimates $\hat{\theta}$ thus yielded unambiguous identifica-

tion of the PSE in each of the two stimulus manifolds, intersecting the supra-second region of the manifold E. The negative shift of the PSE observed in S_6 indicates an asymmetry of the discrimination function; to avoid a possible misunderstanding concerning the method used, we prefer to not name the effect a "time-order error".

Interpretation: retention loss

The observed phenomenon of subjectively perceived equality of physically unequal durations reminds of the "subjective shortening" of retained time intervals, observed in pigeons (Spetch and Wilkie 1983) and in human subjects (Wearden and Ferrara 1993, Wearden et al. 2002). An equivalent of this effect could be the progressive shortening of responses in the duration reproduction task. Therefore, it is natural to attempt an interpretation of the results in terms of the dual klepsydra model (DKM) that successfully accounts for the shortening of reproduced durations. The model assumes internal representation of actually perceived and/or retained durations by accumulation of excitation in temporarily allocated neural assemblies, and a continuous loss of the accumulated excitatory state.

"Retention loss" or "memory trace fading" mechanisms have already been proposed by earlier authors (e.g. Köhler 1923, Lauenstein 1932) to explain response asymmetries in successive comparisons, such as the well-known "time-order error". Despite the influential competition of purely psychological theories (usually variants of the adaptation-level theory: Hellström 1985, 2003, Michels and Helson 1954), the "retention loss" approach is still attractive, as it promises to link psychophysical data with neurophysiological mechanisms. Most "retention loss" theories remained on a level of rather qualitative considerations, while the DKM yields quantitative parameter estimates and allows for testable predictions. By contrast to the "memory trace" theories postulating interactions between the traces of the two stimuli being compared, in the DKM the states of both accumulators evolve independently, without interaction between them.

Starting from an assumption of a functional equivalence between reproduction and discrimination of temporal durations (cf. Introduction), we estimated DKM parameters κ from the PSEs for individual sub-

¹¹ Neither the difference between the PSEs, nor alternative measures of the difference between the partial PMFs in terms of probabilities (Allan 1977, Hellström 1985) provide a complete information on the discrimination function or the shape of the manifold defined by subjective equality.

jects, and for the entire sample. Typical values of $\hat{\kappa}$, estimated from earlier published reproduction data (group averages), were in the order of magnitude 7.5 \times 10⁻³ to 3.3 \times 10⁻² s⁻¹ (Wackermann and Ehm 2006, p. 487). The estimate from the averaged data for all subjects in the present study, $\hat{\kappa} = 3.3 \times 10^{-2} \text{ s}^{-1}$, thus falls at the upper end of the range of earlier groupbased estimates: the corresponding relaxation time of the hypothetical neural accumulators is ~30 s. Concerning individual values: in a later study employing the duration reproduction task, individual $\hat{\kappa}$'s from 3.9 × 10⁻³ to 5.4 × 10⁻² s⁻¹ were obtained from 11 subjects (unpublished data). The $\hat{\kappa}$'s from the present study are dispersed from 2.4×10^{-3} to 6.6 \times 10⁻² s⁻¹, thus approximately in the same range.

The estimates $\hat{\kappa}$ given above are based on the deterministic version of the DKM that assigns a unique response, r, to the stimulus duration s and the inter-stimulus delay w (see Eq. 6). The stochastic version of the DKM specifies, for a given s, a probabilistic distribution of reproduced times and thus accounts for the intra-individual variability of responses (Wackermann and Ehm 2006, p. 486). In the same vein, from the basic assumptions of the stochastic DKM the theoretical probabilistic discrimination function (8), and the partial PMFs for a suitably parameterized stimulus manifold could be derived. These developments exceed the framework of the present study and will be subject of a separate communication.

Summarizing, the present estimates $\hat{\kappa}$ are in a very good agreement with those from previous reproduction studies, although the present values resulted from a heuristic one-point matching procedure. 12 The DKM thus integrates two groups of experimental findings, (i) the negative curvature of reproduction curves, and (ii) the asymmetry of the discrimination function, and provides a unified interpretation of "subjective shortening" or "time-order error" phenomena (as suggested by Wackermann and Ehm 2006, p. 490) in terms of retention loss from hypothetical neural accumulators. In contrast to cognitive-psychological explanatory approaches, operating with concepts of "adaptation level" or "response bias," we assume that these phenomena originate at a proto-cognitive level and reflect the properties of neurophysiological processes underlying the intra-organismic representation of temporal durations.

CONCLUSIONS

Human discrimination of time intervals in the suprasecond domain is characterized by (i) a relatively low accuracy, and, for longer durations, (ii) a systematic tendency to underestimation of earlier durations w.r.t. more recent ones, reflecting an asymmetry of the discrimination function. This asymmetry can be explained by a model of internal time representation based on lossy integrators. The results contribute to a unified interpretation of experimental data on human "time perception" obtained with two different methods, namely, pair-wise comparison and reproduction of time intervals.

LIST OF ABBREVIATIONS

DILL	5 111 1 11
DKM	Dual klepsydra model
JND	Just noticeable difference
PMF	Psychometric function
PSE	Point of subjective equality
RSE	Ratio of subjective equality
WF	Weber fraction

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¹² The reproduction-discrimination equivalence should be, of course, tested in a separate study, combining both tasks on the same cohort of subjects. Incidentally, one participant in the present study participated later in a duration reproduction experiment. The individual estimate from the reproduction data (three sessions, total 105 reproductions of durations in the range 3 to 24 s) was $\hat{\kappa} = 0.038 \text{ s}^{-1}$; the present estimate from the discrimination experiment is $\hat{\kappa}$ =0.041 s⁻¹ (Table II, entry #8). Although this observation is merely anecdotal, the relative stability of these individual values is encouraging.

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