RESEARCH ARTICLE

Intelligence and temporal accuracy of behaviour: unique and shared associations with reaction time and motor timing

Linus Holm · Fredrik Ullén · Guy Madison

Abstract Intelligence is associated with accuracy in a wide range of timing tasks. One source of such associations is likely to be individual differences in top-down control, e.g., sustained attention, that influence performance in both temporal tasks and other cognitively controlled behaviours. In addition, we have studied relations between intelligence and a simple rhythmic motor task, isochronous serial interval production (ISIP), and found a substantial component of that relation, which is independent of fluctuations in top-down control. The main purpose of the present study was to investigate whether such bottom-up mechanisms are involved also in the relation between intelligence and reaction time (RT) tasks. We thus investigated whether common variance between the ISIP and RT tasks underlies their respective associations with intelligence. Two hundred and twelve participants performed a simple RT task, a choice RT task and the ISIP task. Intelligence was assessed with the Raven SPM Plus. The analysed timing variables included mean and variability in the RT tasks and two variance components in the ISIP task. As predicted, RT and ISIP variables were associated with intelligence. The timing variables were positively intercorrelated, and a principal component analysis revealed a substantial first principal component that was strongly related to all timing variables, and positively correlated with intelligence. Furthermore, a commonality analysis demonstrated that the relations between intelligence and the timing variables involved a commonality between the timing variables as well as unique contributions from choice RT and ISIP. We discuss possible implications of these findings and argue that they support our main hypothesis, i.e., that relations between intelligence and RT tasks have a bottom-up component.

Keywords Intelligence · Timing · Cognitive processing · Executive functions

Introduction

Performance on cognitive tasks correlates positively, and there is a growing consensus that the latent factors underlying these correlations form a hierarchically organized structure of abilities, with psychometric intelligence, or *g*, as the most general factor (Jensen 1998; Deary 2000; McGrew 2009). The notion that intelligence is related to individual differences in timing of behaviour, and in particular speed of information processing, goes back to the pioneer days of intelligence research (Galton 1908). A large body of empirical studies has since confirmed that mean reaction time (RT) in a range of cognitive tasks is negatively correlated with psychometric intelligence (Deary 2000; Jensen 2006). The magnitude of this association is generally larger for more complex choice RT (CRT) tasks than for simple RT (SRT) (Lemmon 1927–1928; Jensen 1998). Also, the trial-to-trial variability in RT, operationalized, e.g., as the standard deviation of RT (RTSD), is negatively related to intelligence (Berkson and Baumeister 1967; Jensen 1992; Deary et al. 2001). Mean RT and RTSD are highly correlated with each other, and multivariate commonality analyses with intelligence as dependent variable and RT and RTSD as independent variables show that a large proportion of the explained

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variance in intelligence is common to both RT and RTSD (Jensen 1992). Temporal variability of behaviour on a millisecond scale thus appears to be related both to speed of processing in elementary cognitive tasks and to intelligence.

This association between intelligence and timing accuracy has been further explored using tasks that involve mental manipulation of temporal information, such as duration discrimination, temporal judgment and rhythm perception. Performance on such tasks is positively related to intelligence (Rammsayer and Brandler 2002; Helmbold and Rammsayer 2006; Helmbold et al. 2007; Rammsayer and Brandler 2007; Troche and Rammsayer 2009), and the timing tasks are also positively correlated with each other as well as with mean RT and RTSD in RT tasks (Rammsayer and Brandler 2002; Rammsayer and Brandler 2007). Analyses using structural equation modelling support that a common latent variable, which could be tentatively described as a general temporal accuracy factor, mediate the observed relations (Helmbold et al. 2007).

Why, then, is intelligence related to temporal accuracy? We have stressed the importance of distinguishing between two general types of explanations (Ullén et al. 2008; Madison et al. 2009). The first type involves top-down mechanisms. On this account, the observed relations are mediated by individual differences in executive functions, e.g., attention to task. Indeed, it appears plausible that this explains part of the findings. Temporal discrimination tasks involve manipulation of temporal information in working memory and can thus be assumed to load on executive functions (Kyllonen and Christal 1990; Rammsayer and Brandler 2002; Rammsayer and Brandler 2007). There is extensive evidence that RT tasks depend on attention, which in turn is substantially correlated with intelligence (Schweizer and Moosbrugger 2004; Schweizer et al. 2005). RT tasks are impaired under dual task (Telford 1931; Pashler 1994), and they, at all levels of task complexity, recruit fronto-striatal brain regions that are known to be involved in cognitive control and working memory (D'Esposito et al. 2000; Schluter et al. 2001; Gilbert et al. 2006). There are also more specific indications that attention is involved in the relations between timing tasks and intelligence. The RT × intelligence relation obeys the so called Worst Performance Rule, which states that the worst (slowest) RT trials performed by an individual, i.e., the trials most likely to be affected by attentional lapses, show the strongest association with intelligence (Coyle 2003). As noted, more complex RT tasks show a stronger correlation with intelligence (Jensen 1998); typically, a more complex decision space is also associated with a higher executive load (Rowe et al. 2000). Finally, both temporal and non-temporal discrimination tasks are related to intelligence, and these relations show a substantial commonality which

is likely to reflect general purpose top-down mechanisms (Troche and Rammsayer 2009).

It should be noted that the top-down explanations discussed previously imply that intelligence-timing relations are merely a special case of a more general phenomenon, i.e., that instability in executive functions influences cognitively controlled behaviours. If this were the only type of mechanism at play, it could in fact well be that temporal variability is merely epiphenomenal to fluctuations in attention. It is, therefore, important to examine whether a second type of mechanism, which we may call bottom-up, is also involved. The essential ingredient in a bottom-up explanation is that temporal stability of neural activity has a causal influence on the cognitive processes involved in intelligence. We have investigated this issue using a simple motor timing behaviour, isochronous serial interval production (ISIP), where the participants produce self-paced tapping movements with an even beat. The temporal variability of the produced intervals can be divided into local tap-to-tap variability (Local) and slow drift in tapping frequency (Drift) (Madison 2001; Madison et al. 2009). We have earlier argued that Drift depends on short-term memory of previously performed intervals and is likely to be more sensitive to top-down influences than Local, which appears to reflects unsystematic random noise (Madison 2001; Madison and Delignières 2009). ISIP variability is negatively related to intelligence. Several findings support that this association has a bottom-up component. First, millisecond variability in the ISIP is largely subliminal and relatively inaccessible to top-down control. Recent data from our group indicate that ISIP variability is essentially unaffected by attentional sharing under dual task. Responses to auditory distractors (Repp 2006) and subliminal perturbations (Madison and Merker 2004) are unconscious and involuntary. The ISIP task is self-paced, but one can note that work on tapping in synchrony with an external stimulus suggests that both subliminal and supraliminal processes are involved in motor timing, with the former being important for correction of phase errors and the latter for correction of errors in tapping period (Repp 2005).

Second, relations with intelligence are as strong or stronger for Local than for Drift (Ullén et al. 2008; Madison et al. 2009). In line with this, children with attention deficit hyperactivity disorder (ADHD), which have deficits in executive functions, show larger deviations in Drift than in Local (Jucaitė et al. 2008). Third, ISIP × intelligence relations, unlike RT × intelligence relations, exhibit no tendency to follow the Worst Performance Rule discussed earlier: performance in the most accurate and the least accurate ISIP trials correlates equally well with intelligence (Madison et al. 2009). Fourth, relations between ISIP and intelligence are strongest for durations below 1 s (Madison

et al. 2009), while cognitive control is more important for discrete, non-motor timing tasks that involve multisecond durations (Lewis and Miall 2003). Finally, influencing top-down control by manipulations of state motivation appears not to influence the magnitude of relations between ISIP and intelligence (Ullén and Madison 2009). Taken together, these findings provide convergent evidence that variability in top-down control is not a major source of the ISIP × intelligence association. Accordingly, the association is likely to be partly bottom-up in nature.

In summary, both top-down processes and bottom-up processes are likely to be involved in associations between intelligence and performance on chronometric tasks. More specifically, we can hypothesize that bottom-up mechanisms are of some importance for all tasks requiring temporal accuracy. They may be the dominating factor for the Local component of ISIP. Top-down mechanisms, on the other hand, most likely contribute to relations between intelligence and cognitive timing tasks, including RT tasks. Here, we examined relations between intelligence and three timing tasks: ISIP, SRT and CRT. ISIP variance was partitioned into Local and Drift. Both the central tendency (median) and the variability (interquartile range) of RT were analysed for the SRT and CRT tasks.

To assess the relations between intelligence and the timing variables, we first examined raw correlations between the different performance variables, as well as a stepwise regression of intelligence on the temporal variables. The main hypothesis of the study, given the background summarized previously, was that a common factor underlies relations between intelligence and all timing variables, including Local. This hypothesis was first examined with a commonality analysis, based on a multiple regression of intelligence on those timing variables that showed a significant raw correlation with intelligence. Secondly, we as a complement performed a principal component analysis of the timing variables. The main purpose of this analysis was to test whether the first principal component, which can be regarded as a proxy for a common factor among the timing variables (Jensen and Weng 1994), has a statistically significant association with intelligence.

Materials and methods

Participants

Participants were recruited by advertisements in local newspapers. One hundred and twelve individuals (78 women) participated in the study (age M = 27.1, SD = 7.1 years). Inclusion criteria were normal hearing, good health, and no current or past neurological conditions.

All participants gave informed consent to participate. The study was approved by the Ethical Committe of Umeå University (Dnr 09-065 Ö) and in compliance with The Code of Ethics of the World Medical Association (Declaration of Helsinki).

Material

The standard paper-and-pencil version of Raven's Standard Progressive Matrices Plus (SPM Plus) (Raven et al. 2000) was used to assess intelligence. This test mainly measures psychometric general intelligence (Gustafsson 1984; Jensen 1998). For the timing tasks, custom designed software was used to control sound stimulus presentation and participant response recording. The software was run under Windows XP with a minimal installation and no network or other applications running in the background. The software was furthermore optimized for minimal temporal variability in conjunction with dot.net and directx subroutines, which resulted in system variability with a standard deviation of less than 3 ms. Responses were given by pressing keys on the computer keyboard. SRT and CRT tasks were assessed using auditorily presented tone cues. Stimuli consisted of sampled real sounds presented Peltor HTB7A sound-attenuated headphones at 78 dBA sound pressure level. The sounds have a sharp attack and a relatively fast decay, resulting in a supra-threshold duration of approximately 80 ms. Three different sounds were used, a cowbell for the ISIP and SRT tasks, and a car horn and breaking glass for the CRT task. The reasons for using real sounds are that they are perceptually salient, thanks to their broad spectrum, have a clearly defined onset, thanks to their envelope, and have worked very well in a number of previous studies (see (Madison and Delignières 2009) with references).

Procedure

Participants were tested individually in two sessions. In the first session, the Raven SPM Plus was administered untimed, according to the instructions (Raven et al. 2000). The test took 40–90 min to complete.

The second session consisted of the chronometric tasks (ISIP, SRT and CRT) and was completed individually. The participant was seated upright in front of the computer monitor on a chair with the feet on the floor. In the SRT task, participants were instructed to respond as fast as possible to the auditory stimulus by pressing the space key on the keyboard with the dominant hand. The CRT task was a two-choice RT task. The participants were instructed to press one of two response keys with either the left or the right hand, depending on the stimulus sound (car horn or breaking glass). In each ISIP trial, the participant first

synchronized right hand tapping movements with a number of isochronous stimulus sounds and then continued to tap at the same pace after the sounds had stopped. Only data from the later self-paced continuation phase were used in the analyses.

The participant first performed one supervised practice trial of each of the three tasks together with the experimenter, who made sure the participant understood the tasks. If not, additional instruction was provided and the training was repeated. After this introduction, the participant was left alone with the computer, to perform unsupervised training trials, intended to give the participant a basic level of proficiency with the tasks and were not used in the analyses. The training trials consisted of 1 run of 14 SRT trials, 1 run of 22 CRT trials and 5 ISIP trials. After each CRT trial, feedback was given to the participant on whether the response was correct or incorrect. For both SRT and CRT, the fore periods (i.e. response-to-stimulus intervals) were sampled from a uniform random distribution from 2.3 to 4 s. The 5 ISIP trials consisted of 25 beats synchronized to the stimulus sounds followed by 30 beats in the continuation phase. Stimulus inter-onset intervals (IOIs) of 268, 655, 335, 419 and 524 ms, respectively, were used in the 5 trials. Shorter ISIP trials and IOIs were used than in the experiment proper to save time.

After this practicing trials, the experiment proper began. It consisted of 2 SRT runs of 40 trials each, 2 CRT runs of 40 trials each and 16 ISIP trials. The task order was counterbalanced between participants. The fore period for both SRT and CRT trials was random, as during the practicing trials. Each ISIP trial consisted of 30 synchronization taps followed by 40 continuation taps, using one of the eight IOIs from the geometric series 419, 469, 524, 586, 655, 733, 819 and 916 ms. There were two trials for each IOI, hence 16 ISIP trials in total. In addition to these ISIP trials, subsets of participants performed different additional ISIP trials with long IOIs (1,024 and 1,431 ms), which will be used for other analyses and reported elsewhere. Performance on the ISIP tasks reported here was highly consistent across participant subsets. Participant subset mean differences on ISIP variability constituted a few per cent of the total variation, and there was no statistically reliable difference between the participant subsets on the aggregated Local and Drift performance, as tested with two sample t-tests. Therefore, data from all participant subsets were used and are reported together.

Statistical analyses

Data from practice trials were excluded from all analyses. Due to the typical non-normal distribution of RTs (Luce 1986), the median and the interquartile range were used as estimates of central tendency and variability of RT, respectively. We denote these variables as SRT-M and SRT-IQR for simple RT, and CRT-M and CRT-IQR for two-choice RT. For the ISIP trials, data from the self-paced continuation phase, excluding the five first tapping intervals, were analysed (Madison 2001). Intervals smaller than 200 ms or larger than 1,600 ms were replaced by a moving average over seven intervals, centred on the outlier.

ISIP variability was separated into Local and Drift variability, as described previously (Madison 2001; Madison et al. 2009). In brief, Local was calculated for each trial as:

$$\text{Local} = \frac{1}{\bar{x}} \sqrt{\frac{\sum_1^{N-2} (x_{i+2} - x_i)^2}{2(N-2)}}$$

where x_i is the duration of the temporal interval between beat i and beat $i + 1$, $\bar{x}$ is the mean of all intervals of the trial, and N is the number of intervals in a trial (i.e. 34). Drift is by definition the remaining part of the variance and mainly represents gradual changes in tapping frequency (Madison 2006):

$$\text{Drift} = \frac{1}{\bar{x}} \sqrt{\sigma^2 - \frac{\sum_1^{N-2} (x_{i+2} - x_i)^2}{2(N-2)}}$$

Variables are notated as for Local; σ^2 refers to the total variance in a trial. For Local and Drift, within-participant mean values across all trials and IOIs were used in the analyses.

Stepwise regression techniques were used to analyse the contributions of the different timing variables to intelligence. A forward stepwise regression was performed with intelligence as dependent variable, all timing variables as independent variables, and a significant ($P < .05$) change in total variance explained (ΔR^2) as criterion for entrance or removal of an independent variable. This was complemented with a best subset regression to determine the optimal subset of regressors as measured by Mallows' C_p statistic, which reflects not only the total variance explained but also collinearities between the regressors (Mallows 1973).

Secondly, a commonality analysis was performed to determine the proportion of the total variance in intelligence associated with common and unique effects of the different timing variables (Seibold and McPhee 1979). Only the timing variables that showed significant zero-order correlations with intelligence were included as independent variables in this analysis, i.e., CRT-IQR, Local and Drift. The commonality of all three variables (CRT-IQR, Local and Drift), commonalities of pairs of two variables (CRT-IQR, Local; CRT-IQR, Drift; Local, Drift) as well as unique contributions of each variable were
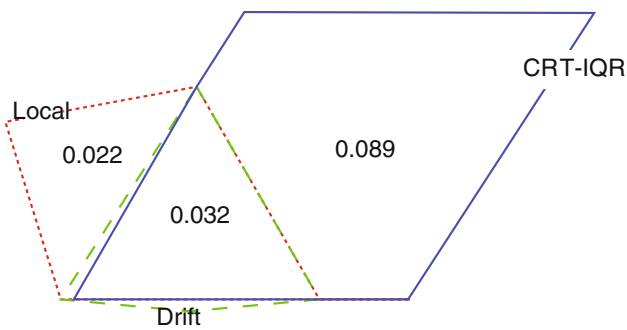
Fig. 1 Venn diagram of timing-related variance components in intelligence. *Graphical* representation of the commonality analysis in Table 3 as a Venn diagram. Each *polygon* represents an independent variable, as indicated in the figure. The bounded subregions formed by their intersections represent unique and common variance components. The area of each subregion is proportional to the amount of variance explained by the corresponding component (see Table 3). There are three large components, i.e., the commonality of all three variables, and unique contributions of CRT-IQR and Local

calculated using linear combinations of the multiple regression coefficients between intelligence and different subsets of independent variables, according to Seibold and McPhee (1979). The results of this analysis were represented graphically (see Fig. 1) as an area proportional Venn diagram, using the technique of Rodgers et al. (2010).

Finally, a principal component analysis was performed on all six timing variables. This analysis revealed two principal components with eigenvalues above 1. Scores on these two components were correlated with intelligence.

Results

Descriptive statistics of intelligence scores and all timing variables are summarized in Table 1. Zero-order

Table 1 Descriptive statistics of all performance variables

Variable	Mean	SD	Min	Max
SPM	45.3	5.6	30	57
SRT-M	209	31	158	302
SRT-IQR	47	18	17	123
CRT-M	432	85	312	887
CRT-IQR	139	51	54	354
Local	4.6	1.4	2.0	9.1
Drift	1.6	.71	.27	3.7

SPM raw score on the Raven SPM Plus test, *SRT-M* median RT score on the simple RT task, *SRT-IQR* RT interquartile range on the simple RT task, *CRT-M* median RT score on the choice RT task, *CRT-IQR* RT interquartile range on the choice RT task, *Local* local variability in the ISIP task, *Drift* drift variability in the ISIP task. Values for all chronometric variables are in milliseconds

correlations between the variables are presented in Table 2. The timing variables generally show positive intercorrelations. Intelligence was negatively related to the ISIP variables and the CRT variables, with a near significant trend for CRT-M ($P = .06$). There were no associations between intelligence and the simple RT variables (SRT-M and SRT-IQR).

The relation between intelligence and the timing variables was first analysed using a forward stepwise regression. Intelligence was used as a dependent variable, and all six timing variables (Table 2) were used as independent variables. CRT-IQR was the single strongest predictor of intelligence, explaining 12.1% (R^2) of the total variance [$F(1, 110) = 15.1$; $P = .0002$]. Adding Local to the model explained an additional 2.4% of variance, but this increase in R^2 only showed a trend for significance [$F(1, 109) = 3.07$; $P = .08$]. None of the other timing variables significantly increased the explained variance in intelligence. A best subset regression confirmed that CRT-IQR and Local constituted the optimal subset of two timing variables in predicting intelligence (Mallows' $C_p = 1.97$).

These findings clearly suggest that shared variance between timing variables plays a role for the observed correlations between individual variables and intelligence. This was confirmed by a commonality analysis with intelligence as dependent variable, and CRT-IQR, Local, and Drift as independent variables (Fig. 1; Table 3). In this analysis, the explained variance in intelligence is partitioned into components consisting of unique contributions of the individual timing variables, common contributions of pairs of two timing variables and one commonality of all three timing variables. The partitions are illustrated graphically in an area proportional Venn diagram in Fig. 1. CRT-M was not included in this analysis, since it only showed a close to significant association with intelligence and since the complexity of commonality analyses—i.e., the number of separate variance components—grows exponentially with the number of independent variables. The total R^2 for this model was 14.7%. As can be seen in Table 3, three variance components clearly stand out as important predictors of intelligence: unique contributions of CRT-IQR and Local are responsible for 60 and 15% of the total variance explained, while the commonality between all three variables contributes 22%. Each of the remaining compartments only contributes around 1% or less.

To further examine the relation between a common latent factor among the temporal variables and intelligence, a principal component analysis (PCA) of the timing variables was performed. The results of this analysis are summarized in Table 4. All six timing variables (see Table 1) were entered into the analysis, which gave two principal components (PC1 and PC2) with eigenvalues

Table 2 Zero-order correlations (Pearson r) between the performance variables

	SRT-M	SRT-IQR	CRT-M	CRT-IQR	Local	Drift
SPM	−.065	−.050	−.18[†]	−.35***	−.24**	−.19*
SRT-M		.63***	.39***	.23**	.22*	.071
SRT-IQR			.35***	.27**	.27**	.11
CRT-M				.62***	.26**	.27**
CRT-IQR					.25**	.39***
Local						.64***

Abbreviations as in Table 1 and text

* $P \le .05$

** $P \le .01$

*** $P \le .0001$ (family wise significant after Bonferroni correction for all 21 tests)

[†] Trend at $P = .06$

Table 3 Commonality analysis of associations between intelligence and timing

	Variance explained (R^2)	Proportion of total explained variance (%)
Unique contributions		
CRT-IQR	.089	60
Local	.022	15
Drift	.0019	1
Commonalities		
CRT-IQR, local, drift	.032	22
CRT-IQR, local	−.00028	−0.2
CRT-IQR, drift	.00062	0.4
Local, drift	.0017	1

Variables are abbreviated as in Table 1 and text. Intelligence was the dependent variable, and CRT-IQR, Local, and Drift were independent variables

Table 4 Principal component analysis of the temporal variables

	PC1	PC2
Eigenvalue	2.67	1.33
Explained proportion of variance	44.4%	22.2%
Correlations with performance variables		
SPM	.27**	−.15
SRT-M	−.63***	−.58***
SRT-IQR	−.65***	−.52***
CRT-M	−.75***	−.12
CRT-IQR	−.71***	.11
Local	−.65***	.48***
Drift	−.60***	.68***

Eigenvalues, per cent variance explained and correlations (Pearson r values) with performance variables are shown for the two principal components with eigenvalues above 1

* $P \le .05$

** $P \le .01$

*** $P \le .0001$

above 1. PC1 was significantly correlated with intelligence and also showed strong relations to all six timing variables. PC2 had oppositely signed associations with the ISIP variables and the SRT variables, but no significant relation to intelligence or the CRT variables.

Discussion

Bottom-up components in associations between timing and intelligence

Behaviours that involve processing of temporal information are correlated with each other as well as with psychometric intelligence. This holds true for RT tasks (Deary 2000; Jensen 2006), motor timing (Ullén et al. 2008; Madison et al. 2009) and cognitive timing tasks (Rammsayer and Brandler 2002; Rammsayer and Brandler 2007). In the present study, we have investigated three timed

behaviours: a simple, repetitive motor timing task (ISIP) and two RT tasks (SRT and CRT). The overall findings are in line with earlier studies, in that we find associations between performance variables for the different timing tasks. With exception for the SRT task, we also find significant relations between performance variables and intelligence. Null or weak relations between SRT and intelligence are not uncommon, and performance in more complex choice RT tasks typically has a stronger relation to intelligence than does SRT (Jensen 1998; Rammsayer and Brandler 2007).

The most important novel finding of the study is arguably that, as predicted, a common source of variance contributes to all observed relations between the timing variables and intelligence. This is supported by the principal component analysis of the timing variables. PC1 was

substantially correlated with all timing variables and also showed a significant relation to intelligence. One should note that while PC1 can be used as a proxy for a common source of variance among a set of intercorrelated variables, a principal component analysis does not separate shared and unique sources of variance among the variables (Jensen and Weng 1994). However, the commonality analysis of the regression of intelligence on CRT-IQR, Local and Drift confirmed that around 20% of the total variance explained was due to a commonality between all three variables rather than unique contributions.

Importantly, these findings suggest that common mechanisms contribute to relations between intelligence and RT tasks on the one hand and relations between intelligence and a simple, repetitive motor task—the ISIP—on the other hand. Whether these common mechanisms are bottom-up or top-down in nature is not something that can be determined from the present findings alone. However, earlier findings make it likely that bottom-up mechanisms are involved. Specifically, we have argued that a series of observations (see Introduction) make it likely that associations between the subliminal Local component of ISIP variability and intelligence are independent of top-down cognitive control (Madison et al. 2009). Since the Local component overlaps with CRT-IQR, it appears likely that bottom-up mechanisms are involved in relations between RT stability and intelligence as well. Even for a cognitive timing task such as the CRT, which certainly involves fronto-parietal circuits for attention and decision making (D'Esposito et al. 2000; Schluter et al. 2001; Gilbert et al. 2006), relations to intelligence may thus in part depend on millisecond temporal accuracy of neural activity that itself is not merely an artefact of attentional fluctuations. We have earlier suggested that these bottom-up mechanisms may represent basic neural design features that influence temporal accuracy in both timing tasks and neural processes of importance for cognition (Ullén et al. 2008; Madison et al. 2009). Precise timing of neuronal firing is of importance for information processing in cortical neuronal networks (Tiesinga et al. 2008) as well as neural plasticity (Kampa et al. 2007). It thus appears conceivable that individual differences in the temporal precision of neural activity could influence both cognitive processing and performance in simple timing tasks such as the ISIP. More specifically, millisecond synchronization of discharges in neuronal ensembles has been suggested as a mechanism to bind different aspects of sensory percept as well as cognitive contents (Singer 1999). Individual differences in gamma synchronization may be related to intelligence and feature binding (Stankov et al. 2006; Keizer et al. 2010). However, more work is clearly needed to understand the mechanisms underlying the associations between intelligence and timing variability.

Unique contributions of timing variables to intelligence

CRT-IQR and Local made substantial unique contributions to intelligence. In fact, the stepwise regression showed that CRT-IQR on its own—i.e., its shared and unique components taken together—explained such a large proportion of intelligence variance and that Local only provided a borderline significant additional contribution. We suggest that the strong relation between CRT-IQR and intelligence reflects that this association depends on the bottom-up mechanisms discussed earlier, as well as on individual differences in top-down control that influence both CRT and intellectual performance. Attentional systems show strong relations to intelligence (Schweizer and Moosbrugger 2004; Schweizer et al. 2005). There is also strong evidence that CRT performance depends on attention: CRT shows interference under dual task (Telford 1931; Pashler 1994), involves fronto-striatal networks of importance for top-down control (D'Esposito et al. 2000; Schluter et al. 2001; Gilbert et al. 2006), and its relations to intelligence follow the Worst Performance Rule (Coyle 2003).

However, the unique contribution of CRT-IQR may of course not exclusively reflect top-down control. CRT is in some senses the most complex of the tasks employed in the present study, since it involves both an expectation and a decision. Another possibility is, therefore, that this behaviour involves more extensive neural circuitry and thus is more sensitive to distributed neural factors that influence temporal accuracy. Along the same lines, the unique contribution of Local could reflect the recruitment of specific neural circuitry for rhythm production, e.g., in sensorimotor areas of the brain (Zatorre et al. 2007). We have earlier suggested that the Drift component of ISIP variability reflects processing of previously produced intervals in short-term memory and that it, therefore, may be more sensitive to top-down control than Local (Forsman et al. 2009; Madison and Delignières 2009). It may, therefore, seem surprising that there was essentially no unique contribution of Drift to intelligence. One explanation could be that top-down components of Drift were captured by the commonality with CRT-IQR.

Concluding remarks

Temporal variability in the millisecond range is related to cognitive performance. The present findings suggest that these relations in part depend on general factors that influence accuracy in different types of timing tasks and that are unlikely to simply reflect attentional slips or other individual differences in top-down control. In total, temporal accuracy appears to explain around 15% of the variance in intelligence. Only a yet smaller fraction of this

appears likely to reflect 'timing per se', i.e., bottom-up factors that influence neural temporal accuracy in both timing tasks and cognitive processing. However, this should perhaps not be seen as unexpected or discouraging. Even if general intelligence is unitary as a statistical construct, its biological basis appears to involve hundreds, if not thousands, of individual genes, each of which makes but a minute contribution to variability in the phenotype (Plomin 2006). As we study simple physiological or behavioural phenomena that are associated with intelligence, we might expect a similarly complex jigsaw puzzle, where each component mechanism is only a small part of the complete picture.

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