



Correlations between intelligence and components of serial timing variability

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ABSTRACT

Psychometric intelligence correlates with reaction time in elementary cognitive tasks, as well as with performance in time discrimination and judgment tasks. It has remained unclear, however, to what extent these correlations are due to top-down mechanisms, such as attention, and bottom-up mechanisms, i.e. basic neural properties that influence both temporal accuracy and cognitive processes. Here, we assessed correlations between intelligence (Raven SPM Plus) and performance in isochronous serial interval production, a simple, automatic timing task where participants first make movements in synchrony with an isochronous sequence of sounds and then continue with self-paced production to produce a sequence of intervals with the same inter-onset interval (IOI). The target IOI varied across trials. A number of different measures of timing variability were considered, all negatively correlated with intelligence. Across all stimulus IOIs, local interval-to-interval variability correlated more strongly with intelligence than drift, i.e. gradual changes in response IOI. The strongest correlations with intelligence were found for IOIs between 400 and 900 ms, rather than above 1 s, which is typically considered a lower limit for cognitive timing. Furthermore, poor trials, i.e. trials arguably most affected by lapses in attention, did not predict intelligence better than the most accurate trials. We discuss these results in relation to the human timing literature, and argue that they support a bottom-up model of the relation between temporal variability of neural activity and intelligence.

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1. Introduction

A number of studies show that there is a relation between intelligence and millisecond variability in timed behaviors. Intelligence is thus negatively related to the variability as well as the mean of reaction time (RT) in a wide range of elementary cognitive tasks (Deary, 2000; Jensen, 2006). The correlation between RT variability and intelligence is often larger than the correlation between mean RT and intelligence (Baumeister, 1998; Jensen, 1992). Recent studies combining choice RT tasks and temporal discrimination tasks also demonstrate that the discrimination tasks show higher correlations with intelligence than do RT and RT variability,

and that the portion of intelligence explained by the RT tasks predominantly represents variance also explained by the temporal tasks (Helmbold, Troche, & Rammsayer, 2007; Rammsayer & Brandler, 2007).

But why would temporal variability be related to intelligence? One can think of two broad but not mutually exclusive types of explanations. The first type is bottom-up models where certain basic neural properties influence the amount of temporal variability in neural activity. This variability is in turn reflected both in timing tasks and in the quality of cognitive processing. Top-down types of explanations, in contrast, involve some higher-order component of the neural system, such as attention, that affects both timing and cognitive performance. The main purpose of this study was to further explore the relation between intelligence and temporal variability and to elucidate the underlying nature of this relation. Specifically, correlations were assessed between

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intelligence and timing performance in a simple timing task – isochronous serial interval production – for different variability components and for different durations of the interval to be timed.

Separating between bottom-up and top-down mechanisms is theoretically important because it addresses the neural basis of intelligence. A purely top-down model would mean that there is no causal relation between intellectual performance and timing variability *per se*. The lower temporal variability of more intelligent persons could, in this case, be due to more effective higher-order control mechanisms that are used both in timing tasks and in problem solving: for example, less intelligent people could exhibit more temporal variability because they have more frequent lapses of attention. On a bottom-up account, in contrast, temporal accuracy of neural activity is one of the biological underpinnings of intelligence: it is measurable as behavioral variability in simple timing tasks, but more importantly has a causal effect on the neural processes that are involved in cognition.

The timing tasks employed in previous studies of the relation between timing performance and intelligence make it difficult to distinguish between the contribution of top-down and bottom-up mechanisms because they conceivably involve both. Temporal discrimination and judgment tasks obviously require decision making and processing of information in working memory. Even elementary cognitive tasks are to a large extent dependent upon decision criteria, however, as evidenced by early responses (sometimes even before the stimulus) and substantial effects of manipulating the time between trials (Grosjean, Rosenbaum, & Elsingher, 2001).

One way of approaching this problem is to determine whether intelligence is related to performance in a simple timing task in which temporal variability is largely the result of automatic processes that are inaccessible to conscious control. If this is the case, it would provide support for a bottom-up account of the relation between intelligence and temporal variability. To this end isochronous serial interval production (ISIP) was employed as a model behavior. ISIP is also known as self-paced tapping or continuation tapping, and consists of making regular, i.e. isochronous movements, typically using the index finger or a drum stick. In each ISIP trial, the participant first beats in synchrony with an isochronous sequence of stimulus sounds (synchronization) and then self-paced at the same rate after the sounds cease (continuation) (Stevens, 1886). The standard deviation (SD) of the intervals produced during the continuation phase is the most common measure of variability.

Several observations support that millisecond variability in ISIP is controlled by neural processes that are relatively unaffected by top-down control mechanisms. First, ISIP – unlike temporal judgment and discrimination tasks – does not include explicit instructions to process temporal information in working memory. Second, ISIP qualifies as an automatic rather than a cognitive timing task according to the classification of automatic and cognitive temporal processing recently provided by Lewis and Miall (2003). According to their meta-analysis, three task characteristics in particular favor an automatic rather than cognitive mode of processing: (i) the use of temporal intervals shorter than 1 s; (ii) intervals appearing repetitively in continuous succession;

and (iii) involvement of motor production. ISIP with interval durations in the sub-second range fulfils all three criteria. Third, a number of findings show that participants have limited conscious control of ISIP variability: perturbations in ISIP performance by distractor sounds occur involuntarily and without conscious awareness (Repp, 2006); the timing of movements are affected by subliminal perturbations of pacing stimuli (Madison & Merker, 2004); and participants automatically track sound sequences in which intervals gradually change by an unnoticeable amount (Madison & Merker, 2005). Fourth, other tasks show very little interference with ISIP. Remarkably, ISIP variability thus only shows a marginal increase during a concurrent choice reaction time task (Michon, 1966) or speech production (Nagasaki, 1990).

In addition, correlations between intelligence and ISIP variability can be subjected to more detailed analyses that shed further light on the nature of the intelligence-timing relation. First, ISIP variance can be partitioned into components (Madison, 2001; Vorberg & Wing, 1996) that likely have different control mechanisms, i.e. higher-order phenomena such as drift (gradual change of tempo) and local interval-to-interval variability. The relationship of drift and local variability to intelligence can thus be studied separately. This is of interest in the sense that deficits in attention or other top-down control processes arguably should be noticeable in drift and other higher-order dependencies at least as much as in local variability. For example, the difference in variability between children with attention-deficit hyperactivity disorder (ADHD) and normally developing children was substantially larger for drift than for local variability (Jucaité, Dahlström, Farde, Forssberg, & Madison, submitted for publication). Second, the relation between intelligence and variability can be studied for different inter-onset intervals (IOIs) of the pacing stimuli in the synchronization phase. This is useful in two ways: (i) trials with different IOIs can be regarded as replications, and if similar relations between intelligence and timing are seen across IOIs it indicates that the relation is robust; (ii) in relation to the previously mentioned meta-analysis of Lewis and Miall (2003), if a relation between intelligence and variability is found for IOIs in the sub-second range, this would provide additional evidence for that the intelligence-timing relation is not only due to differences in top-down control. Third, it is commonly found that on multi-trial elementary cognitive tasks, such as choice reaction time tasks, the worst performance trials predict intelligence better than best performance trials (the “worst performance rule”) (Coyle, 2003). Is an analogue of the worst performance rule found for ISIP? The answer to this question gives important information about the nature of the intelligence-timing relation. If a worst performance rule is found, it would mean that trials with high variability – i.e. trials where momentary attentional lapses may have impaired performance – are better predictors of intelligence than the trials where the participant performed optimally. This scenario suggests that top-down mechanisms may play an important role for the intelligence-timing relation. If no worst performance rule is found, on the other hand, it would appear that attentional lapses are not responsible for correlations between intelligence and variability. In this case, it would rather appear that the relation is primarily due to bottom-up mechanisms, i.e. temporal variability in

neural activity that is present in all trials regardless of fluctuations in attention.

The present study consists of two experiments. In both experiments, intelligence was measured with an untimed administration of the Raven SPM Plus. ISIP data was collected individually from each subject. In Experiment 1, the participants consisted of males that were in addition subjected to brain morphometry by means of magnetic resonance imaging. The imaging results are reported elsewhere (Ullén, Forsman, Blom, Karabanov, & Madison, 2008). Correlations between intelligence and components of ISIP variability (drift and local variability) were investigated for different IOIs. To investigate whether a worst performance rule was present, produced intervals were also sorted within each trial according to temporal accuracy, and correlations with intelligence were investigated separately for intervals of different accuracy. These analyses showed that local variability was more strongly negatively correlated with intelligence than drift for all IOIs, and revealed no evidence for a worst performance rule. The main purpose of Experiment 2 was to replicate these findings in a new sample of both males and females, and to extend the design by including also longer IOIs (> 1 s).

2. Experiment 1

2.1. Methods

2.1.1. Participants

Participants were recruited from the public by local newspaper advertisements. Thirty-six right-handed, Caucasian males (age 19–49 years; mean 32.8, and SD 8.3 years) with no history of neurological disease participated in the study. There was a wide range of musical experience among the participants, but none was a professional musician. The experimental procedures were undertaken with the understanding and written consent of each participant, conforming to The Code of Ethics of the World Medical Association (Declaration of Helsinki). Ethical approval was given by the Karolinska Hospital Ethical Committee (Dnr 2005/320-32).

2.1.2. Materials

All aspects of the ISIP task were controlled by custom designed software running on a PC with a real-time operating system. An Alesis D4 drum module connected via MIDI to the PC produced the sounds and collected the responses. The temporal resolution of the system was 1 ms. Stimuli consisted of 20 sampled cowbell sounds presented in isochronous sequence through Peltor HTB7A sound-attenuated headphones at 78 dBA sound pressure level. The last two sounds were attenuated to 72 and 66 dBA, respectively, to reduce the startle reaction when stimuli cease. The sounds have a sharp attack and a relatively fast decay, resulting in a supra-threshold duration of approximately 80 ms. Responses were given by beating a drumstick against a drum pad with a piezoelectric element.

A paper-and-pencil version of Raven's Standard Progressive Matrices Plus (SPM Plus) (Raven, Raven, & Court, 2000) was used to measure intelligence.

2.1.3. Procedure

Each participant was tested individually, sitting upright on a chair with the feet to the floor. The ISIP task was performed

first. In each ISIP trial, the participant synchronized right hand movements with 20 stimulus sounds, and then continued to beat another 45 times without interruption after the sounds had stopped. This procedure was repeated for each trial, which had one of seven different stimulus inter-onset intervals (IOIs) according to a geometric series (215, 300, 375, 469, 586, 733, and 916 ms). The first block was for practice and consisted of 7 trials, one for each IOI. The second block was the experiment proper that consisted of 14 trials, two for each IOI. IOIs were presented in a different random order within each block for each participant. The two blocks took 30–40 min to complete.

After the ISIP task participants were offered a break of about 10 min. They were then subjected to the Raven SPM Plus (untimed), which took between 40 and 120 min to complete.

2.1.4. Dependent measure computation

For the ISIP task, all data from the practice trials were ignored. For the experimental trials, data from the continuation phase, excluding the first five data points, were analyzed. Excluding the first five data points of the continuation phase is a standard procedure in ISIP research to exclude possible behavioral artifacts during the transition from synchronization to continuation (Madison, 2001). Thus, the 39 time intervals between the last 40 beats in each continuation phase were analyzed. Outlier intervals were excluded according to the following procedure. A moving average (MA) was computed on those of seven successive intervals in the response series that were within the range 200–1600 ms. Intervals outside this range were considered unintentional errors, being either close to simple reaction time or the limit for experiencing temporal recurrence (Mates, Radil, Müller, & Pöppel, 1994), which was the basis for the present task. Such errors were very rare and consisted mostly of detection failures in the data acquisition process, that is, either double-triggering with an interval of 0–50 ms or failed triggerings with double or triple the stimulus interval. If the number of valid intervals within a 7-point window were less than 3, the MA was assigned the value of the stimulus interval. Intervals 50% shorter or longer than the MA were replaced with the MA, disregarding the outlier itself. This way, the outlier criterion was mainly related to the intervals actually produced, accounting for possible drift in the mean. The typical SD for adults is on the order of 5% of the interval; the 50% limit should therefore be transgressed very rarely, and does therefore not constitute filtering of the data.

The raw number of correct items in the Raven SPM Plus was used as a measure of intelligence.

2.1.5. Local and drift variability

The total variance in ISIP data can be partitioned into different components. One source of variability is drift, i.e. gradual changes in ISIP intervals. This should be distinguished from local variability, i.e. variability in the duration of consecutive intervals. Here, these two variance components were estimated separately (see Appendix). Local variability (Local) was estimated as the variance of difference scores between temporal intervals two intervals apart, i.e. with a lag 2 difference. This estimate is thus minimally influenced by drift. Local was estimated from difference scores between

intervals with a lag 2 difference, rather than a lag 1 difference (i.e. consecutive intervals), for the following reason. Consecutive intervals in ISIP are negatively correlated. This lag 1 negative autocorrelation may reflect feedback error correction, where short produced intervals tend to be followed by longer ones and vice versa (Madison, 2000). It would be inappropriate to let a measure of local variability reflect this error correction process, which in fact is important for stable performance. Therefore lag 2 difference scores were used. Drift was estimated as the remaining portion of the variance, i.e. total variance – local variance, which consists mainly of the aforementioned drift in the mean interval (Madison, 2001, 2006).

2.1.6. Worst performance rule like variability

The same lag 2 difference scores that were used in the calculation of Local were also used to test whether an analogue of the worst performance rule in RT tasks (Coyle, 2003) is present in ISIP. The following procedure was used. First, within each trial, the 36 lag 2 interval differences were rank ordered, disregarding sign, and divided into four bins with 9 data points in each. The first bin would thus contain the intervals with the smallest difference scores, i.e. the most accurate intervals of a trial. The next bin would contain less accurate intervals, and so on, with the least accurate intervals sorted into the last bin. Secondly, the coefficient of variation (CV) of each bin was computed. Third, the means of these CVs were calculated across trials within-participant, resulting in four mean CV values for each participant. Finally, the correlations between intelligence and mean CV were calculated separately for each of these four bins. If a worst performance rule like phenomenon was present, correlations with intelligence would increase from the first bin that contains the smallest interval differences (i.e. the best performance), to the last bin that contains the largest interval differences.

2.2. Results and discussion

Two participants were omitted as outliers due to their erratic ISIP sequences, which yielded extreme variability estimates even after correction of outlier intervals. All the following analyses were based on the remaining 34 participants. The group mean Raven score was 47.2 (range 34–58, SD 6.57), which corresponds approximately to the 75th percentile according to 1999 norms for Germany (Raven et al., 2000). Aggregated CV across stimulus IOIs were computed for each variability estimate and participant: Local was 3.62 (range 2.19–6.05, SD 0.76), and Drift was 2.17 (range 1.04–4.89, SD 1.02).

The correlations between intelligence (raw and age-corrected Raven scores) and all relevant variability measures are shown in Table 1. A scatterplot of the correlation between intelligence and Local is shown in Fig. 1A. Intelligence was not correlated with age ($r = -0.04$; n.s.). For comparison, the total variability in terms of the coefficient of variation is also included in the table ($CV(\text{total}) = SD / \text{mean} \times 100$).

All bins of the worst performance rule measures, including the fourth bin (WPR 4) with highest variability (i.e. worst performance), were slightly less correlated with intelligence than was Local. There was no trend that correlations with

Table 1

Correlations between intelligence and ISIP variability components in Experiment 1 ($N = 34$)

| | ISIP variability component | | | | | | |
|-----------------------------|----------------------------|-------|-------|-------|-------|-------|-------|
| | CV(total) | Local | Drift | WPR 1 | WPR 2 | WPR 3 | WPR 4 |
| Raven scores | -0.42 | -0.44 | -0.41 | -0.41 | -0.36 | -0.37 | -0.38 |
| Raven scores, age corrected | -0.43 | -0.45 | -0.42 | -0.39 | -0.37 | -0.39 | -0.38 |

All correlations were significant at $p < 0.05$. Variability measures are mean values within-participant across all replications and IOIs. Abbreviations: CV (total), the total coefficient variation; Local, local variability; Drift, drift variability; WPR 1–4, local variability in worst performance rule bins 1–4. For further explanations of the variability measures see Methods and Appendix.

intelligence increased for bins with higher variability, as can be gleaned from comparing the four bins from the smallest (WPR 1) to the largest (WPR 4) variability (all p -values above 0.8 for tests of difference between r -values). We thus found no indication of a worst performance rule in ISIP.

To explore the role of IOI, correlations between intelligence and the two variability components, Local and Drift, were computed separately for each IOI (Fig. 1B). Across the whole range of IOIs, stronger negative correlations were found with Local than with Drift. A trend can be observed for Local that render correlations computed for the four longest IOIs significant but those computed for the three shortest IOIs non-significant.

One possibility would be that trivial scaling effects influence differences in correlations between IOIs. For example, it appears possible that the component of timing variability that is related to intelligence is attenuated by other noise components, and that the proportion between these might vary as a function of IOI. To address this issue, means of Local and Drift as a function of IOI were computed. As can be seen in Fig. 1C, Local and Drift behave quite differently as a function of IOI than the previously described correlations. In particular, the fact that Local is almost constant at 3.6% across IOIs speaks against that a scaling effect would explain the pattern of correlations between Local and intelligence. As seen in Fig. 1B, this correlation is almost zero for 215 ms IOI and increases monotonically with IOI to -0.5 for 916 ms IOI. Local thus accounts for a substantially larger correlation with intelligence than does Drift, although the aggregate correlations across IOIs of these two variables are quite similar (-0.44 and -0.41 , respectively, for non age-corrected Raven scores; Table 1). In contrast, Drift is larger for 733 and 916 ms IOI (Fig. 1C). This is consistent with a scaling effect that may influence correlations between Drift and intelligence scores.

Experiment 1 was based on a relatively small sample ($n = 34$), so some of the differences between IOIs could be due to chance. On the other hand can trials with different IOIs be seen as replications, and the fact that Local was more strongly related to intelligence than Drift for all IOIs indicates that the finding is quite robust.

3. Experiment 2

Experiment 1 suggested a trend for higher correlations between local variability and intelligence as a function of IOI. This is of particular importance since timing of durations

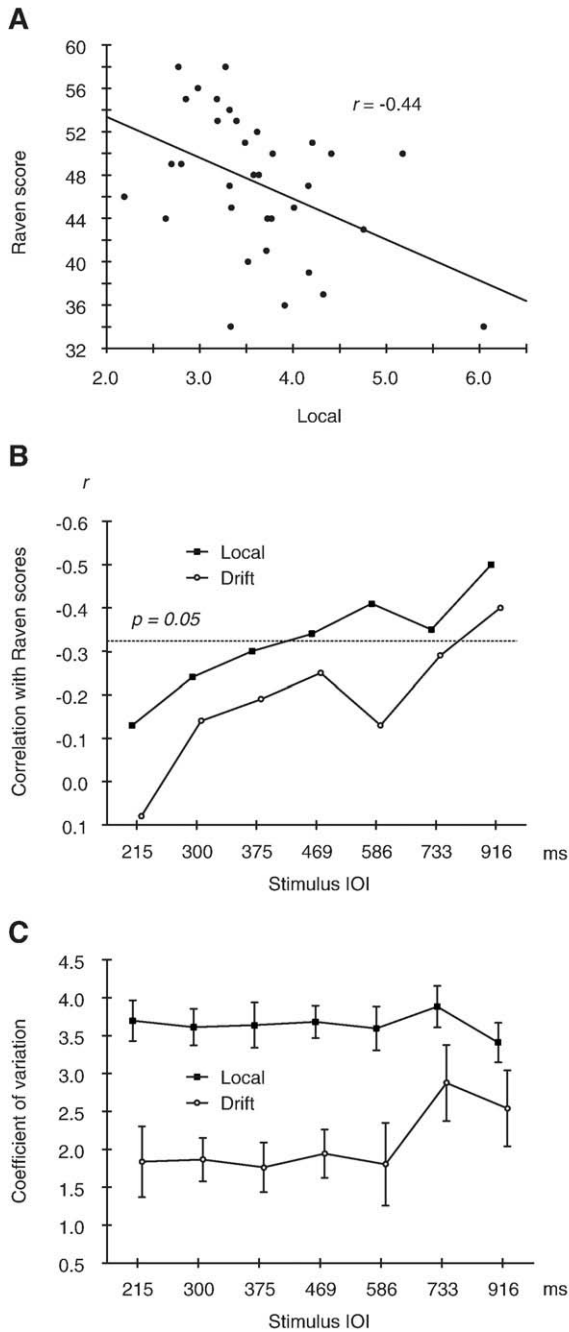


Fig. 1. Local and Drift variability in Experiment 1. (A) Scatterplot of the relation between Raven scores and Local. The correlation had an r -value of -0.44 . (B) Correlations between the Local and Drift components of ISIP variability and intelligence calculated separately for each IOI. The dashed line indicates the 0.05 level of significance. (C) Local and Drift as a function of IOI.

above around 1 s has been suggested to be more cognitive in nature (see Introduction). The main purpose of Experiment 2 was to explore this phenomenon further, in addition to providing a replication of the main findings in Experiment 1. The range of IOIs was thus extended to 1280 ms in Experiment 2. In addition, one intermediate level of IOI was added between each level of IOI employed in Experiment 1.

3.1. Methods

Dependent measure computations, materials, and procedure were the same as in Experiment 1, except that a wider range of IOIs was employed, the synchronization stimuli were 30 instead of 20, and there were 12 instead of 7 practice trials.

3.1.1. Participants

Twenty women and 10 men were recruited from the public by local billboard and newspaper advertisements (age 19–62 years, mean 32.8, and SD 9.9 years). None had a history of neurological disease or had participated in Experiment 1. The musical experience varied in the group, but no participant had more than one year of musical education or was a regular performer of music. Handedness was not considered since neuroanatomical analyses were not to be performed. All participants were Caucasian. A written consent was obtained from each participant, and ethical considerations and approval were the same as in Experiment 1.

3.1.2. Materials and procedure

The participant synchronized movements of the preferred hand with 30 stimulus sounds, and then continued to beat another 45 times without interruption after the sounds had stopped. This procedure was repeated for a total of 46 trials: The experiment proper block with 17 different IOIs according to a geometric series (215, 240, 268, 300, 335, 375, 419, 469, 524, 586, 655, 733, 819, 916, 1024, 1145, and 1280 ms) was preceded by a practice block with a subset of 6 IOIs (215, 300, 419, 586, 819, 1145 ms), all conditions occurring twice and presented in a different random order for each participant.

3.2. Results and discussion

The group mean Raven score was 42.5 (range 27–59, SD 6.66), which corresponds approximately to the 50th percentile according to 1999 norms for Germany (Raven et al., 2000). This group was therefore more similar to the general population, and this difference between participants across experiments was significant (one-way ANOVA; $F(1, 62) = 10.19$; $p = 0.002$). Mean aggregated CV for each participant across stimulus IOIs were very close, and only slightly smaller than those obtained in Experiment 1: Local was 3.53 (range 2.31–4.77, SD 0.64), and Drift was 1.84 (range 0.97–3.19, SD 0.53). The differences in CV between the experiments were not significant ($p > 0.10$). Although the lower intelligence of Experiment 2 participants would predict higher mean variability,

Table 2

Correlations between intelligence and ISIP variability components in Experiment 2 ($N = 30$)

| | ISIP variability component | | | | | | |
|-----------------------------|----------------------------|--------|-------|--------|--------|--------|--------|
| | CV(total) | Local | Drift | WPR 1 | WPR 2 | WPR 3 | WPR 4 |
| Raven scores | -0.38* | -0.44* | -0.36 | -0.41* | -0.38* | -0.39* | -0.40* |
| Raven scores, age corrected | -0.36 | -0.42* | -0.35 | -0.40* | -0.38* | -0.39* | -0.38* |

*Correlations significant at $p < 0.05$. Variability measures are mean values within-participant across all replications and IOIs. Abbreviations: CV(total), the total coefficient variation; Local, local variability; Drift, drift variability; WPR1–4, local variability in worst performance rule bins 1–4. For further explanations of the variability measures see Methods Appendix.

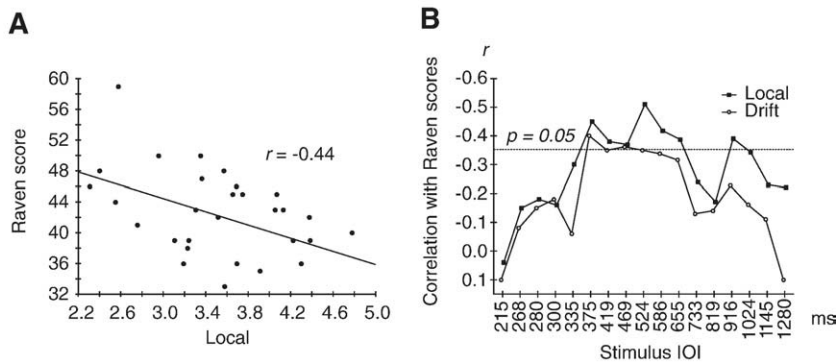


Fig. 2. Local and Drift correlations with intelligence in Experiment 2. (A) Scatterplot of the relation between Raven scores and Local. The correlation had an r -value of -0.44 . (B) Correlations between the Local and Drift components of ISIP variability and intelligence calculated separately for each IOI. The dashed line indicates the 0.05 level of significance.

we believe that the larger numbers of both practice and experimental trials (12 and 34 vs. 5 and 14 in Experiment 1) may have facilitated performance. Mean CV as a function of IOI also exhibits the same pattern as seen in Fig. 1B, namely that Local is constant at 3.5% whereas Drift increases from around 1.5 to 2% between 586 and 733 ms IOI (with 655 ms exhibiting an intermediate value of 1.85). Drift did not increase any further above 733 ms.

Correlations between intelligence and variability measures are shown in Table 2. A scatterplot of the correlation between intelligence and Local is shown in Fig. 2A. Age-corrected scores did not yield higher correlations with ISIP variability, in spite of an $r = -0.30$ negative correlation between Raven scores and age. This is substantially higher than in Experiment 1 and might be accounted for by the wider age range in this sample. The correlation is somewhat steeper than in Experiment 1 ($r = -0.44$), in accord with the wider range of Raven scores. In the WPR analysis there was, as in Experiment 1, no trend that correlations with intelligence increased for bins with higher variability (all p -values above 0.8 for tests of difference between r -values).

Fig. 2B shows correlations between intelligence and Local and Drift as a function of IOI. The pattern is similar to that obtained in Experiment 1, both in magnitude and shape, except that the slope of change is steeper in the range 300–400 ms. Importantly, the correlations do not increase for the extended range of IOIs, but tend rather to decrease across the range 1024–1280 ms. As can be seen, the tendency for a non-monotonic function of IOI between 586 and 916 ms (i.e. a smaller correlation for 733 ms) found in Experiment 1 (Fig. 1B) was replicated. While such a scattering of correlation coefficients may well be due to chance alone, this tendency is further reinforced by its replication for 819 ms, the latter IOI being included only in Experiment 2.

4. General discussion

4.1. Timing variability and intelligence – arguments for a bottom-up relation

We found that variability in a simple, automatic timing task – isochronous interval production – is negatively correlated with intelligence. All variability components considered

exhibited negative correlations with intelligence, but local interval-to-interval variability, Local, had the highest predictive power across inter-onset intervals (IOIs) in both experiments. Notably, the largest correlations were observed for an intermediate range of IOIs from about 500 to 900 ms.

We argue that several findings in this study, taken in conjunction with earlier literature, favor that bottom-up mechanisms are involved in the relation between intelligence and variability. First, the mere fact that local variability in the ISIP correlates with intelligence supports a bottom-up mechanism. As mentioned in the Introduction, the earlier literature shows that millisecond variability in the ISIP is both subliminal and relatively inaccessible to top-down control: responses to distractors are unconscious and involuntary (Repp, 2006), responses occur to subliminal perturbations (Madison & Merker, 2004, 2005), and ISIP variability shows only marginal interference effects in dual task situations (Michon, 1966; Nagasaki, 1990). Secondly, deficits in attention or other top-down control processes should be noticeable in higher-order dependencies such as drift at least as much as in local interval-to-interval variability. What we found is, on the contrary, that higher-order dependencies consistently contribute less to the variance in intelligence than does local variability. Third, we found no support for a worst performance rule in ISIP. In other words, there was no indication that trials with high variability – i.e. the trials where momentary attentional lapses may have impaired performance – were better predictors of intelligence than the trials where the participant performed optimally. Fourth, correlations with intelligence were strongest for durations below 1 s, i.e. for durations shorter than those typically controlled by cognitive timing systems (Lewis & Miall, 2003).

4.2. Putative neural mechanisms of the intelligence–timing relation

Behavioral data thus show that local ISIP variability is relatively independent of cognitive control. In line with this, neuroimaging studies of brain activity suggest that ISIP loads relatively little on the fronto-parietal association areas that are known to be implicated in highly g -loaded problem solving tasks (Jung & Haier, 2007). Brain activation during ISIP and related tasks is rather found in a network of brain regions

including primary sensorimotor cortex, the supplementary and pre-supplementary motor areas and lateral premotor areas in the frontal lobe, auditory regions in the superior temporal gyrus and, subcortically, the basal ganglia and the cerebellum (Jäncke, Loose, Lutz, Specht, & Shah, 2000); for reviews see Rao et al. (1997) and Zatorre, Chen, and Penhune (2007). Activity in prefrontal regions is typically higher in more cognitive timing tasks, i.e. tasks that involve discrete durations rather than repetitive patterns, long durations (> 1 s) and no motor production (Lewis & Miall, 2003).

Neural activation studies thus provide further support for the idea that the relation between ISIP variability and intelligence is not mainly due to differences in top-down mechanisms. However, this also raises a puzzling question. If there is relatively little overlap in brain activity between ISIP and problem solving tasks, how could ISIP variability play a causal role for intelligence? We suggest that the answer may be that local ISIP variability reflects a general level of temporal variability in the neural activity of the brain. This variability can be measured as local variability during ISIP but, we propose, is also present more broadly in neural processes that are involved in cognition. Support for this idea is found in that ISIP variability is substantially correlated with performance in cognitive timing tasks (Keele, Pokorný, Corcos, & Ivry, 1985).

Obviously the potential sources of temporal variability and noise in neural activity are multifarious and occur at different levels, from ion channels to neuronal network properties (Faisal, Selen, & Wolpert, 2008). We recently investigated neuroanatomical correlates of ISIP variability and intelligence, and found that both higher temporal accuracy and higher intelligence were related to larger volume of prefrontal white matter in overlapping regions (Ullén et al., 2008). The white matter contains connections between brain regions. These findings suggest that the amount of prefrontal connectivity may be one common factor underlying both ISIP variability and intelligence. A more specific hypothesis in line with Jung and Haier's parieto-frontal model of intelligence (Jung & Haier, 2007) is thus that individual differences in variability of neuronal activity in fronto-parietal circuits are important for intelligence, and reflected as variability in the ISIP. It should also be noted, however, that anatomical correlates of intelligence are widespread and found in all brain lobes (Haier, Jung, Yeo, Head, & Alkire, 2004, 2005; Johnson, Jung, Colom, & Haier, 2008; Jung & Haier, 2007; Ullén et al., 2008). It is therefore possible that other regions, e.g. in the temporal lobe, that are known to be involved in rhythmic control (Zatorre et al., 2007), are also of importance for the variability-intelligence relation.

More work is needed to understand how temporal variability could underlie intelligence. We would like to mention two generic possibilities, however. First, a large literature demonstrates that precise and reliable timing of neuronal firing is of importance for information processing in cortical neuronal networks (for a review see e.g. Tiesinga, Fellous, & Sejnowski, 2008). More specifically, Singer (1999) has suggested that millisecond level synchronization of discharges in neuronal ensembles is a mechanism to dynamically represent both sensory percepts and cognitive contents. Abnormal patterns of neuronal synchronization are associated with cognitive deficits in both schizophrenia and Alzheimer's disease (Uhlhaas & Singer, 2006). Secondly, millisecond differences in the timing of pre- and post-synaptic neuronal action potentials have pro-

found influences on synaptic plasticity (Kampa, Letzkus, & Stuart, 2007). A relation between intelligence and neural plasticity is suggested by the fact that "general learning ability", i.e. the common factor underlying the positive co-variation among a battery of learning tasks, is highly related to general intelligence (Jensen, 1998). For a comprehensive discussion of individual differences in neural plasticity as a possible factor underlying intelligence, see Garlick (2002).

4.3. The role of inter-onset interval in the relation between ISIP variability and intelligence

A secondary focus of the present study was the influence of the interval to be timed. Intuitively, one might think that the processing of very brief intervals would be a measure of cognitive speed (Jensen, 1987), and that the processing of long intervals would be a measure of cognitive ability (Lewis & Miall, 2006). In contrast, our results indicate that ISIP within a quite narrow, intermediate range from approximately 400 to 900 ms yields the highest correlation with intelligence. Interestingly, this is also approximately the range within which ISIP performance is optimal, i.e. has the smallest coefficient of variation (Fraisse, 1982; van Noorden & Moelants, 1999). The fact that correlations with intelligence were strongest within a particular range also speaks against that they would reflect variability in motor execution.

At the lower end of the IOI range, relative variability is larger for durations shorter than 300–350 ms (Hibi, 1983; Peters, 1989). Possibly, this breakpoint reflects a larger involvement of the cerebellum for shorter intervals (Miall & Reckess, 2002; Riecker, Wildgruber, Mathiak, Grodd, & Ackermann, 2003). On the upper end of the IOI range, the 1 s breakpoint reviewed by Lewis and Miall (2003) is supported by numerous studies that demonstrate a qualitative difference in timing between intervals shorter and longer than around 1 s (Madison, 2001, 2006). In conclusion, the approximate 400 and 900 ms limits for the IOI range found to yield the highest correlations with intelligence are likely to be related to switching between underlying mechanisms and strategies, probably because this range provides the most optimal conditions and therefore the smallest intrinsic error variability.

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Appendix A. Estimation of variance components in ISIP data

The total variance in ISIP data was partitioned into two components. The first component, *Local*, was calculated for each trial as:

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

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. 39). The expression inside the square root is a variance measure based on local differences between data points. Because ISIP sequences are known to exhibit lag 1 negative autocorrelation, i.e. consecutive intervals are negatively correlated (Vorberg & Wing, 1996), lag 2 instead of lag 1 differences are used. This is also why the term $N-2$ must be employed in the denominator. Furthermore, as far as random data are considered, sequential differences are on average twice as large as differences from the mean, which is why the denominator is $2(N-2)$. Finally, the square root of this variance measure (corresponding to a standard deviation) is divided by the mean duration of all intervals in the trial, to make Local comparable to a coefficient of variation.

Similarly, we computed an estimate for the remaining part of the variance, *Drift*, which consists mainly of gradual changes in ISIP inter-onset intervals (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.

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