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The genetic architecture of correlations between perceptual timing, motor timing, and intelligence

Miriam A. Mosing [a,b], Karin J.H. Verweij [a], Guy Madison [c], Fredrik Ullén [a,*]

[a] Department of Neuroscience, Karolinska Institutet, SE-171 77 Stockholm, Sweden
[b] Department of Genetic Epidemiology and Biostatistics, Karolinska Institutet, SE-171 77 Stockholm, Sweden
[c] Department of Psychology, Umeå University, SE-901 87 Umeå, Sweden

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ABSTRACT

Psychometric intelligence correlates with performance on a wide range of sensory and motor tasks that involve processing of temporal information in the millisecond-second range. For some timing tasks, e.g. reaction time and discrimination of temporal stimuli in working memory, the associations with intelligence are likely to involve top–down mechanisms such as attention. However, studies on repetitive, automatic motor timing tasks indicate that correlations between intelligence and timing also may reflect bottom-up mechanisms, i.e. basic neural properties that influence both the temporal accuracy of behavior and cognitive processes. Here, we study the genetic architecture of the associations between intelligence, perceptual timing (auditory rhythm discrimination) and motor timing (finger tapping) in a large twin cohort. Specifically, we hypothesized that the associations between these tasks on the phenotypic level involve broad pleiotropic genetic effects that influence all three tasks, as well as additional genetic effects on the covariation between perceptual and motor timing. Phenotypic associations between the variables were low to moderate, with Pearson's correlations in the range 0.17–0.32. Trivariate twin modeling showed that the associations between the three variables were essentially due to shared genetic influences. In support of the hypotheses, we found evidence for pleiotropic effects on motor timing, perceptual timing, and intelligence, as well as additional genetic covariation between the two timing tasks that was not shared with intelligence. We conclude, first, that genetic factors underlying intelligence may involve genes which influence brain properties of importance for the temporal accuracy of neural processing. We discuss possible neural substrates of such effects. Secondly, the correlation between motor and perceptual timing also partly explained by genetic influences that are unrelated to intelligence.

1. Introduction

Intelligence is correlated with performance in a range of behaviors that involve timing in the millisecond to second range. The most well-studied type of task in this context is presumably reaction time, where the participant produces a response (e.g. a key press) to a sensory stimulus in some modality (Jensen, 2006; Luce, 1986). A large variety of such paradigms have been employed, from simple reaction time, where both stimuli and responses are identical across trials, to complex choice reaction time tasks where several response alternatives are available, and the selection of the appropriate response may depend on instructions, stimulus features, and previous knowledge stored in long-term memory. To give an example, one common design of a choice reaction time task is that visual stimuli (e.g. from light emitting diodes) appear in two or more possible spatial positions; there is one response button corresponding to each stimulus position, and the participant responds by pressing the correct button (Jensen, 2006). Consistent findings in the literature are that the mean and the inter-trial variability of reaction time correlate negatively with intelligence, and that correlations tend to be larger for more complex tasks (Jensen, 2006; Sheppard, 2008). Sheppard (2008), in a comprehensive review of studies reporting correlations between reaction time and general intelligence, found average correlations for different reaction time paradigms to range between −0.22 and −0.40, with stronger associations for paradigms involving more choice alternatives. In a population representative sample of 900 Scottish individuals, Deary and coworkers found correlations with intelligence of −0.31 for simple reaction time, −0.49 for 4-choice reaction time, and −0.26 for intraindividual trial-to-trial variability (standard deviation) of reaction time in both tasks (Deary, Der, & Ford, 2001).

Another chronometric task which has been frequently studied in relation to intelligence, is the inspection time task (Grudnik & Kranzler,

* Corresponding author at: Department of Neuroscience, Retzius väg 8, Karolinska Institutet, SE-171 77 Stockholm, Sweden.
E-mail address: Fredrik.Ullen@ki.se (F. Ullén).

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2001; Vickers, Nettelbeck, & Willson, 1972). In a standard version of this paradigm, a π-shaped visual stimulus with two parallel vertical lines connected by a horizontal line at the top is presented for a brief period of time before it is covered by a masking stimulus. In different trials, the stimulus randomly appears in one of two versions, where either the left or the right vertical line is longer than the other. The task of the participant is to indicate which line is longer by pressing one of two response buttons. Inspection time has been interpreted as a measure of visual processing speed, and can be considered as an example of a visual backward masking task, where the perceptual processing of a briefly presented target stimulus is influenced by the subsequent presentation of a masking stimulus; also other backward masking tasks, using e.g. alphanumeric stimuli, correlate with intelligence (Burns & Nettelbeck, 2003; Burns, Nettelbeck, & White, 1998). Unlike in a reaction time task, in inspection time only the timing of the target and mask stimuli are timed, not the responses of the participant. The stimulus duration is modified from trial to trial, using an adaptive procedure, in order to estimate the participant's inspection time. This is conventionally defined as the stimulus duration at which the participant makes a correct discrimination with a certain predefined probability (commonly chosen as 97.5%; Jensen, 2006). Correlations between inspection time and intelligence typically fall in the same range as for reaction time, i.e. between −0.2 and −0.4 (Grudnik & Kranzler, 2001; Sheppard, 2008). Auditory versions of the inspection time task have been constructed; these show similar relations to intelligence (Bates, 2005; Sheppard, 2008).

Here, we will focus on a third type of timing task that has been studied in relation to intelligence: perceptual and motor paradigms where the task involves processing and discriminating durations and rhythmic structures. Rammsayer and coworkers have demonstrated that intelligence correlates with performance on various perceptual timing tasks, including duration discrimination of single intervals, rhythm perception, temporal order judgment, and temporal generalization (Helmbold, Troche, & Rammsayer, 2007; Rammsayer & Brandler, 2002; Troche & Rammsayer, 2009). As for reaction time and inspection time, correlations between accuracy in these tasks and measures of intelligence typically fall in the range 0.2–0.4 (Haldemann, Stauffer, Troche, & Rammsayer, 2011; Rammsayer & Brandler, 2002, 2007). Similar correlations have been found between rhythm discrimination subscales of music aptitude tests and intelligence (Lynn, Wilson, & Gault, 1989; Mosing, Pedersen, Madison, & Ullén, 2014b; Schellenberg & Weiss, 2013). Associations between motor timing and intelligence have been studied using the isochronous serial interval production (ISIP) paradigm (Madison, 2001) — a simple, repetitive task where the participant performs self-paced isochronous (regular) tapping movements, e.g. with a finger. Several studies have demonstrated that temporal variability in this task, operationalized e.g. as the coefficient of variation of the produced intervals, is negatively correlated with intelligence, with r values typically around −.30 (Holm, Ullén, & Madison, 2011; Madison, Forsman, Blom, Karabanov, & Ullén, 2009; Ullén, Söderlund, Kääriä, & Madison, 2012).

The various timing tasks discussed above are also correlated with each other. Several larger studies have included both reaction time and inspection time, and in psychometric models of cognitive abilities these tasks load significantly on a common broad ability factor (Gt — Reaction and Decision Speed), which is often interpreted as speed of information processing (Johnson & Deary, 2011; McGrew, 2009; Roberts & Stankov, 1999). However, inspection time and reaction time also have independent contributions to intelligence (Kranzler & Jensen, 1991; Nettelbeck & Rabbitt, 1992; Petrill, Luo, Thompson, & Detterman, 2001). Perceptual tasks involving manipulation of temporal information are correlated with reaction time measures – i.e. a faster reaction time is related to better performance in perceptual timing task – with the magnitude of most reported r values in the 0.1–0.3 range (Helmbold et al., 2007; Rammsayer & Brandler, 2002, 2007). Helmbold and coworkers modeled these relations with structural equation modeling, and found good fit for a model where a common temporal factor mediated the effects of both reaction time and perceptual timing on intelligence (Helmbold et al., 2007). Holm and coworkers (Holm et al., 2011) studied relations between motor timing in the ISIP, reaction time, and intelligence. Correlations between reaction time measures and motor timing were mostly in the range 0.2 to 0.4, and a commonality analysis indicated that the associations of these tasks with intelligence involved both overlapping and unique components. When the ISIP task is performed with different effectors by the same individual, reported correlations in motor timing accuracy range from $r = 0.36$ for speech-jaw movement correlations (Franz, Zelaznik, & Smith, 1992) to $r = 0.90$ for finger-forearm correlations (Keele, Ivry, & Pokorny, 1987). A correlation of $r = 0.53$ has been reported between ISIP accuracy and performance in a perceptual timing task (auditory duration discrimination) (Keele, Pokorny, Corcos, & Ivry, 1985). These modest-to-high correlations suggest that common mechanisms could be involved in timing tasks in different modalities.

To summarize, analyses on the phenotypic level suggest that associations between intelligence and timing are weak to moderate in magnitude, and likely to involve common mechanisms as well as more narrow and task specific components. Analyses of timing-intelligence relations in genetically informative samples have mainly focused on reaction time. Early twin studies of reaction time have been reviewed by Jensen (2006) and Beaujean (2005). Jensen (2006) reports a mean heritability of reaction time across studies of 0.44 (SD = 0.19), while the association between reaction time and intelligence appears essentially driven by genetic pleiotropy, i.e. common genes influencing different phenotypic variables (mean genetic correlation = 0.90, SD = 0.13). In a more recent study, Lee and coworkers, in a study of older (age > 65 years) Australian twins, found a genetic correlation of $r = 0.32$ between simple reaction time and intelligence, with overlapping genes explaining a substantial part of the association between the two variables (Lee et al., 2012b). Several twin studies have also been performed on inspection time and intelligence (Luciano et al., 2001, 2004, 2005). Luciano and coworkers (Luciano et al., 2005) analyzed the association between these variables using directional causation modeling, a method which can be used to analyze direction of causation for correlated traits in genetically related individuals, provided that genetic influences on one of the traits are sufficiently different in magnitude from genetic influences on the other trait. The results showed a heritability of 0.57 for inspection time, and that the covariation between the traits was best explained by pleiotropic genetic effects.

A striking feature of this literature is that intelligence is related to performance in a wide range of diverse tasks, that include elementary cognitive tasks measuring information processing speed, perceptual and cognitive tasks involving online manipulation of temporal information, and repetitive rhythmic motor behaviors. With regard to the latter, we have earlier argued that the association between intelligence and rhythmic accuracy in a simple, automatic motor behavior such as the ISIP supports that the intelligence-timing relation may involve bottom-up mechanisms that are distinct in nature from top-down phenomena such as fluctuations in attention (see Discussion) (Holm et al., 2011; Madison et al., 2009; Ullén et al., 2012b). To analyze the biological underpinnings of the association between motor timing and

Table 1
Descriptive statistics for the outcome variables.

	Mean	SD
IQ[a]	12.70	5.33
Rhythm	15.32	2.22
ISIP	4.83	1.39

[a] Values refer to the raw scores on the Wiener Matrizen Test.