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Authors: Yael Salzer, Gilles de Hollander, Birte U. Forstmann

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Sensory neural pathways revisited to unravel the temporal dynamics of the Simon effect: A model-based cognitive neuroscience approach

Yael Salzer*, Gilles de Hollander, and Birte U. Forstmann

University of Amsterdam, Amsterdam, The Netherlands Netherlands Institute for Neuroscience, Amsterdam, The Netherlands

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*Corresponding Author:

Yael Salzer
Nieuwe Achtergracht 129
1018 Amsterdam
Netherlands
salzerit@gmail.com

Highlights

- The temporal dynamics of the Simon effect varies by task's conditions and modality
- The main senses share similar architecture of spatial/non-spatial neural pathways
- As a mathematical model the DMC accounts for the effect's temporal dynamics
- DMC can construct a bridge between neural and behavioral measures of the Simon task
- Model-based cognitive neuroscience provides broad account for the Simon effect

Abstract

The Simon task is one of the most prominent interference tasks and has been extensively studied in experimental psychology and cognitive neuroscience. Despite years of research, the underlying mechanism driving the phenomenon and its temporal dynamics are still disputed. Within the framework of the review, we adopt a model-based cognitive neuroscience approach. We first go over key findings in the literature of the Simon task, discuss competing qualitative cognitive theories and the difficulty of testing them empirically. We then introduce sequential sampling models, a particular class of mathematical cognitive process models. Finally, we argue that the brain architecture accountable for the processing of spatial ('where') and non-spatial (‘what’) information, could constrain these models. We conclude that there is a clear need to bridge neural and behavioral measures, and that mathematical cognitive models may facilitate the construction of this bridge and work towards revealing the underlying mechanisms of the Simon effect.

Keywords: Simon task, model-based cognitive neuroscience, diffusion model for conflict.

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Introducing the Simon effect and its temporal dynamics

The Simon task was first described by Simon and colleagues (Simon and Rudell, 1967; Simon and Small, 1969). It captures an intuitive phenomenon: we perform much better when the source of information and appropriate response are spatially aligned (Fitts and Deininger, 1954). In the original Simon task, participants are asked to identify tones played to their right or left ears. High and low pitch sounds are assigned to right or left keys, as instructed. The spatial location of the auditory stimulus is task-irrelevant. Nevertheless, participants respond faster and more accurately when the appropriate key spatially matches the stimulated ear (i.e., corresponding condition) than when it does not (i.e., non-corresponding condition). The calculated mean difference in response times (RT) and in error rates between the corresponding and non-corresponding conditions is called the *correspondence effect*, or simply, the *Simon effect*. Spatial compatibility effects have been found for auditory (Wascher et al., 2001; Xiong and Proctor, 2016), visual (Forstmann et al., 2008a; see for review Lu and Proctor, 1995), and tactile stimuli (Hasbroucq and Guiard, 1992; Salzer et al., 2014). The effect generalizes to paradigms where the response modality is manipulated: for example when the hands are crossed versus uncrossed (Hommel, 1993; Riggio et al., 1986; Wascher et al., 2001), when using foot pedals (Medina et al., 2014), when using the middle and index fingers of the same hand

(Forstmann et al., 2008c; Hübner and Mishra, 2013; Töbel et al., 2014), when using eye-movements (Duprez et al., 2016; Lugli et al., 2016), and when using hand-reach motor responses (Buetti and Kerzel, 2008; Finkbeiner and Heathcote, 2016; Freud et al., 2013). These studies suggest that the Simon effect is not simply due to which cortical hemisphere encodes the stimulus or controls the response.

Distributional analyses of RT are commonly used to evaluate the temporal dynamics of the Simon effect (De Jong et al., 1994). In distributional analyses, the distributions of RTs for corresponding and non-corresponding trial types are partitioned into quantiles or proportional bins (De Jong et al., 1994; Ratcliff, 1979; Ridderinkhof, 2002). For example, the 0.2 quantile of an RT distribution indicates for which RT 20% of the RTs are faster, the 0.4 quantile indicates for which RT 40% of the RTs are faster, etc. The Simon effect can be defined for each quantile separately: the difference in quantile RTs between the corresponding and non-corresponding trial types. The dynamics of the Simon effect across the distribution can be visualized by plotting the relative effect for each quantile *(e.g., 0.2 quantile of incongruent minus the 0.2 quantile of the congruent)* as a function of the mean RT quantile across conditions. Such a plot is known as a *delta plot* (Ridderinkhof, 2002). The pattern of the change in the effect across the distribution is assumed to provide insight into the temporal dynamics of the processes that underlie the effect (De Jong et al., 1994; Proctor et al., 2011). A typical left-right visual Simon task, in which the participants are asked to recognize a non-spatial dimension of a lateralized visual stimulus (e.g., color or shape), yields a decreasing effect across the RT distribution (see Figure *1*A) (Hedge and

Marsh, 1975; Hommel, 1994; Lu and Proctor, 1995; Ridderinkhof, 2002). The following models have been proposed to explain why.

Dual-route models and the role of cognitive control

De Jong, Liang and Lauber (De Jong et al., 1994) proposed a dual-route model to explain the decreasing delta plots in the Simon task (see Figure *2*). They suggested that two processes take place in parallel. One process refers to a task-relevant indirect route that processes the deliberate response decision based on task demands. The other process refers to a task-irrelevant process, where the spatial code directly activates a response that corresponds with the relative location of the stimulus (Kornblum et al., 1990). In the corresponding condition, both task-relevant and irrelevant dimensions of the stimulus generate the same response. In the non-corresponding condition, the irrelevant response contradicts the correct response because the stimulus onset automatically primes the spatially corresponding (incorrect) response. However, the automatic process is short term and it quickly dissipates (Hommel, 1994; Simon et al., 1976).

The reasoning for the short-term nature of the task-irrelevant direct route activation is still disputed. In his study from 1994, Hommel manipulated two factors, the discriminability of the target and the frequency of non-corresponding trials. As expected, two effects were found. First, the Simon effect decreased, from high to low discriminability, suggesting that while the participants were accumulating the task relevant features, the activation of the spatial response code gradually decayed. Secondly, a higher frequency of non-corresponding trials led to a decrease in the Simon effect, implying that participants adopted a strategy in which the irrelevant-route was dynamically inhibited, depending on task demands (see also Logan and Zbrodoff, 1979). Most importantly, these two effects did not interact, suggesting that spontaneous decay is independent of one's strategy.

Ridderinkhof (Ridderinkhof, 2002) proposed the activation-suppression model, as an alternative account of decay of the Simon effect for longer RTs. The model, which is an elaboration of the dual-route model (De Jong et al., 1994), proposes that for correct completion of the task, an active inhibition process suppresses the task-irrelevant direct route. The decrease in accuracy and the additional time to respond at the non-corresponding trials reflect the additional time and effort required to suppress the interfering task-irrelevant response tendency. To account for the temporal dynamics of the Simon effect, the model suggests that the selective suppression takes time to build up. Hence, the model predicts that fast responses are more vulnerable to impulsiveness and thus tend to be incorrect. This prediction has been validated in various studies that show low accuracy for the fastest quantiles of incongruent trials, followed by a rapid improvement in performance, reaching an asymptote at slower quantiles (Ridderinkhof, 2002; Többel et al., 2014; van den Wildenberg et al., 2010). The model also predicts that slower responses will benefit more from the suppression, which translates to a smaller Simon effect at higher quantiles. Most importantly, Ridderinkhof proposed that the slope of the delta plot at the slowest quantiles is indicative of the strength of the selective suppression; more negative slopes imply stronger suppression (Forstmann et al., 2008c).

The inconsistency of the delta plots – common or separate mechanisms?

The decreasing delta plot has been a hallmark of the horizontal (left-right) visual Simon task. However, not all variations of the Simon task show this particular pattern (see Figure 1). An increase of the Simon effect for longer RTs has been shown for other forms of the task and for other modalities, such as when hands are crossed in a horizontal visual Simon task (Wascher et al., 2001), in vertical visual Simon tasks (Töbel et al., 2014; Wiegand and Wascher, 2007, 2005), auditory Simon tasks (Buetti and Kerzel, 2008; Wascher et al., 2001; Xiong and Proctor, 2016), as well as tactile Simon tasks (Salzer et al., 2014).

Wascher and colleagues (Wascher et al., 2001; Wiegand and Wascher, 2007, 2005) suggested that paradigms showing increasing and decreasing Simon effects are the result of two different processes. They proposed a ‘visuomotor Simon effect’ and a ‘cognitive Simon effect’. The visuomotor Simon effect underlies the standard, visual horizontal Simon task. The visuomotor Simon effect occurs because the task-irrelevant stimulus location of a horizontal visual target automatically activates the corresponding response, via the visuomotor pathway. Its activation quickly fades out and results in a decreasing Simon effect (negative delta plot slope). The Simon effect found in other forms of the Simon task is the product of high-level cognitive interference between two non-decaying processes (i.e., ‘cognitive Simon effect’). In this case, the irrelevant activation does not fade out, therefore the Simon effect increases over time, leading to a positive delta plot slope.

The visuomotor account was used to explain the horizontal visual Simon delta plots, and distinguish it from the cognitive interference mechanism. However, negative delta plot slopes have been found in variants of the Simon task, posing a challenge to Wascher's theory of separate mechanisms (see Figure 1). In a study by Vallesi and colleagues (Vallesi et al., 2005), participants performed a vertical Simon study, where they responded with an up or down key-press to checkerboard figures vertically aligned above or below a fixation cross. The slope of the slowest segment of the delta plot in this study was positive (Buetti and Kerzel, 2008; Töbel et al., 2014; Wiegand and Wascher, 2005). However, in the study of De Jong and colleagues (De Jong et al., 1994) and Wiegand and Wascher (Wiegand and Wascher, 2007), when task instructions were randomized across trials, the vertical Simon effect decreased across the RT distribution. When Wascher and colleagues (Wascher et al., 2001) used high tones (1000 Hz and 1500 Hz) in a horizontally aligned auditory Simon task, the slope of the slowest segment of the delta-plot was positive. Xiong and Proctor (Xiong and Proctor, 2016) found distinctively different slopes for high and low tone frequencies. For high tones the slope reached an asymptote, but for low frequency tones (200 Hz and 500 Hz), the slope of the slowest segment of the delta-plot was negative (see Figure 1B). In a somatosensory Simon study, Salzer and colleagues (Salzer et al., 2014) presented horizontally aligned left and right vibrotactile stimuli on the back of the participant's torso. Here again, the slope of the slowest segment of the delta plot was positive. However, when a centrally positioned neutral vibrotactor was added, the Simon effect decreased across the RT distribution (Exp. 3 in Salzer et al., 2014, see Figure 1C). To summarize, the lack of uniformity in observed delta plots in different task variants and task modalities challenges the attempts to provide a coherent and parsimonious model for the underlying processes (Proctor et al., 2011). It is unclear if and when the Simon effect is driven by a visuomotor automatic mechanism, or is the outcome of a conflict between higher cognitive codes (Proctor et al., 2011; Wiegand and Wascher, 2007).

Various studies have proposed that even though the slopes of the delta plots are different in variants of the task, their underlying mechanism is shared. For example, Töbel and colleagues (Töbel et al., 2014) demonstrated that the correspondence of the previous trial had a similar effect on the delta plots of horizontal and vertical visual Simon tasks. In both tasks, the slopes of the slowest segment of the delta plot decreased more following non-corresponding trials. Also, in both tasks, the accuracy in the fastest quantiles was higher after incongruent trials than it was after congruent trials. Töbel and colleagues interpreted these commonalities as evidence for a common mechanism. Buetti and Kertzel (Buetti and Kerzel, 2008) measured the course of the RT distribution and initial movement angle (IMA) of hand movements, in horizontal visual, vertical visual, and horizontal auditory Simon tasks. They successfully replicated previous findings of negative RT delta plot slopes exclusively in the horizontal visual Simon condition. However, the time course for the IMA delta plot was similar in horizontal visual, vertical visual, and horizontal auditory task conditions. Namely, in all task conditions, the difference between IMA in corresponding and non-corresponding conditions (i.e., the Simon effect in IMAs) decreased with increasing RTs. These studies argue for a single underlying mechanism account as the most parsimonious explanation to the time course of the Simon effect.

To summarize, the dual-route model proposes a general common interference mechanism in which two processes take place at the same time; in one the deliberate response decision is made based on task demands, while in the other the spatial code directly activates a response that corresponds with the relative location of the stimulus (Kornblum et al., 1990). As reviewed here, various pieces of evidence (Buetti and Kerzel, 2010; Töbel et al., 2014) converge in favor of a general common interference mechanism over the account of two separate mechanisms responsible for the negative and positive delta plots, the ‘visuomotor’- and ‘cognitive’-interference mechanisms. However, being qualitative accounts, it is difficult to directly compare them quantitatively (Lewandowsky and Farrell, 2010). Formal mathematical cognitive models provide explicit and precise assumptions when arguing for one mechanism over the other. In the following sections we will argue for the general common interference mechanism. We will first describe formal mathematical cognitive models that describe such a mechanism. Then we will discuss how functional neuroanatomy could constrain these models.

Mathematical cognitive process models of the Simon effect

Mathematical cognitive models offer a means to quantitatively formalize cognitive theories communicated verbally (i.e., qualitative). Unlike descriptive statistical models, such as delta plots, cognitive models are generative models (or “process models”), that provide an account not just of how behavioral data is structured, but also how it could potentially have been generated. One class of mathematical cognitive models particularly suited to better understand the temporal dynamics of the Simon effect are so-called *sequential sampling* models, such as the diffusion decision model (DDM, see Figure 3A; Ratcliff, 1978). These models attempt to describe the temporal mechanisms underlying simple decisions under time pressure, perceptual decision-making, and memory recognition. They assume that a decision is formed by sequentially accumulating evidence for different choice options, until a predetermined threshold is reached for one of them, after which a corresponding response is made. The models make very precise predictions about how certain experimental manipulations should change the shape of RT distributions, as well as error proportions. It has been shown that these models can parsimoniously explain a wide range of experimental effects in decision-making (Forstmann et al., 2016).

Sequential sampling models have great potential to help us understand how irrelevant stimulus properties, such as spatial location, influence decision-making throughout the course of a trial. Strikingly, however, standard sequential sampling models such as the DDM offer no straightforward way to account for the RT distributions found in the Simon task. Servant and colleagues (Servant et al., 2014) attribute this failure to the fact that the Simon task breaks the so-called Wagenmakers-Brown law (Wagenmakers and Brown, 2007). The Wagenmakers-Brown law states that, under many standard conditions, the mean RT and standard deviation (SD) of RT are linearly related. This follows theoretically from the mathematical equations describing the DDM, and has also empirically been found in a large range of cognitive paradigms. In the Simon task, the mean RT of the incongruent condition is larger than the mean RT of the congruent condition, i.e., positive Simon effect. According to the Wagenmakers-Brown law, the SD of the RTs in the incongruent condition should be larger than the SD of the RTs in the congruent condition. Consequently, the difference between the congruent and incongruent conditions would increase for higher quantiles (i.e., the difference in the 0.6 quantile will be larger than the difference in the 0.2 quantile). This should result in a positive delta plot.

However, in the Simon task, the mean RT of the incongruent condition is *higher* than the mean RT of the congruent condition, whereas the standard deviation RT of the incongruent condition is *lower* than the standard deviation RT of the congruent condition. Consequently, the difference between the conditions is smaller for higher quantiles. This phenomenon is also reflected in the negativity of the delta plots' slopes discussed above (Zhang and Kornblum, 1997).

Recently, Ulrich and colleagues (Ulrich et al., 2015) developed an extension of the DDM, called the *diffusion model for conflict tasks* (DMC) that can account for the negative delta plot slopes found in the Simon task, as well as for other conflict tasks (see Figure 3B and 3C). The DMC rests on the dual-route model of two simultaneous parallel processes, the task-relevant route and the automatic task-irrelevant direct route (De Jong et al., 1994; Ridderinkhof, 2002). It assumes that evidence from both routes are superimposed onto a single accumulating process. The accumulation of task-relevant information is modeled as a standard diffusion process, which has a constant rate of accumulation throughout the course of a trial. The accumulation of task-irrelevant information in the automatic process, however, quickly rises in the beginning of a trial, and then slowly decays. The mean diffusion trajectory of the automatic process throughout time is modeled by a Gamma distribution. In the DMC, as proposed by Ulrich and colleagues, both the time-to-peak, as well as the dispersion of the Gamma distribution are (in part) determined by a parameter called τ(tau). Crucially, Ulrich and coworkers showed that, when the DMC is fitted to data of participants that performed conflict tasks, such as the Simon task, τ is the only parameter that meaningfully varies between the tasks. This parameter, representing both the speed-of-onset as well as the decay of the automatic process, thereby solely captures the difference in positive versus negative delta plot slopes in the two tasks.

The fact that the DMC can capture datasets with both positive and negative delta plot slopes by changing just one parameter speaks against the idea of separate ‘visuomotor’ and ‘cognitive’ interference mechanisms, as proposed by Wascher et al. (Wascher et al., 2001). Rather, it suggests a common mechanism, but underlying parameters that differ. The DMC provides evidence that a more positive (negative) delta plot slope means that the automatic process peaks later (earlier) in time and/or influences decision for a longer (shorter) period of time. The DMC is intuitively appealing and the range of behavioral patterns it can parsimoniously account for is impressive. Recent electrophysiological work (Servant et al., 2016) also provided some neural data that supports the proposed dynamics in the model. The DMC still has some limitations, but a discussion of these is beyond the scope of this review.

The DMC, and other cognitive models alike, give us the opportunity to peek into the underlying cognitive mechanisms of the Simon task with greater precision than descriptive statistical tools, like the delta plot, alone. With computational models it is possible to formulate quantitative predictions about behavior that can be empirically tested and falsified. We can refine our understanding of how stimulus-response conflicts arise by asking questions, such as investigating what part of the underlying decision-making mechanisms determines the behavioral difference between the horizontal and vertical Simon tasks. Importantly, we can also use the computational models to ask more precise questions about the neural implementation of these processes: where in the brain could such processes arise, and what kind of signals do we expect to find there (de Hollander et al., 2015; Marr, 1982)?

How do ‘what’ and ‘where’ neural pathways subserve the Simon effect?

Functional neuroanatomy has the potential to constrain the models of the underlying mechanisms in the Simon task. We argue that cognitive models like the DMC can help us better understand the temporal dynamics of the underlying Simon task and that functional neuroanatomy can ground its assumptions in the structure of the brain. We qualitatively link the neural structure of two separate neural pathways that independently process spatial and non-spatial features of the input with mathematical cognitive models. In this section we will introduce the ‘what’ and ‘where’ pathways in three main modalities—visual, auditory, and somatosensory. Ideally, we would like to extend the proposed qualitative links, to empirical work that explicitly tests these links quantitatively in a model-based cognitive neuroscience framework (de Hollander et al., 2015). We discuss how neural measures can be related to the variability in latent cognitive processes described by mathematical cognitive models. We propose a means to examine how and where these processes are implemented in the brain, as well as to distinguish between competing theories that cannot be identified by mere behavioral data alone (de Hollander et al., 2015; Turner et al., 2016).

‘What’ and ‘where’ in the visual system

It is well established that visual information projects from the striate cortex into two parallel extrastriate pathways (Ungerleider and Mishkin, 1982). The ventral ‘what’ pathway, a projection from the striate to the inferior temporal cortex, processes object perception and identification in a hierarchical serial form (see Figure *4*A). The dorsal ‘where’ pathway, a projection from the striate to the occipitoparietal pathway, specializes in spatial perception (Haxby et al., 1991; Ungerleider and Haxby, 1994). An elaboration of this model (Milner and Goodale, 1998) places emphasis on the crucial role the dorsal pathway plays in all dimensions of response action planning, namely ‘where’ and ‘how’ the action will take place (e.g., visual guided movement, eye movement, grasping). The model of the dorsal pathway was further expanded by Kravitz and colleague (Kravitz et al., 2010), who studied non-human primates. The authors suggested that the occipitoparietal pathway projects forward into at least three separate branches—the parietal-prefrontal pathway, parietal-premotor and parietal-medial-temporal pathway—that take part in spatial working memory and declaration, visually-guided action, and navigation, respectively. Recently, Freud and colleagues (Freud et al., 2016) argued that the distinction between the roles of the two pathways is not binary. The dorsal occipitoparietal pathway accounts also for perception and identification processes that are independent of, and have a different role from, the object representation in the occipitotemporal pathway. Freud and colleagues proposed a functional perception–action continuum along the occipitoparietal pathway in which “more-posterior and medial regions support more perceptual representations, and more-anterior and lateral regions are more tuned to action oriented representations” (Freud et al., 2016, p. 774). However, it was denoted that the unique contribution of the occipitoparietal pathway to object representation is not yet settled.

Relating neural measures of the visual system with cognitive models

The brain structure of ‘where’ and ‘what’ pathways constrains the dual-route model of the Simon effect (De Jong et al., 1994). In a way it refutes Wascher and colleagues’ (Wascher et al., 2001) notion of ‘visuomotor’- and ‘cognitive’ interference mechanisms. It is more likely that the spatial location of horizontal stimuli and vertical stimuli are processed by the occipitoparietal ‘where’ pathway, generating the task-irrelevant direct response. At the same time, the occipitotemporal pathway processes the task-relevant feature. A reasonable assumption is that signal propagation within a pathway might vary according to the complexity of the information. It is possible that horizontal information propagates faster or has a clearer and stronger signal than vertical information, and as a result, activates the task-irrelevant response sooner. This hypothesis may be tested with the model-based cognitive neuroscience approach of linking the DMC parameters with temporal neural measures, such as EEG’s markers of activation of the relevant response and inhibition of the irrelevant response, or the onset of covert incorrect electromyography (EMG) bursts and behavioral measures. The onset of covert incorrect EMG burst is particularly interesting since it is a direct measure of a motor response that was initiated but eventually aborted (i.e., partial error; Servant et al., 2016). One could predict that an early onset of partial error in the horizontal Simon task would correlate with the DMC τ parameter and the negative delta plot slope. Similarly, a later partial error onset in the vertical Simon task is expected to correlate with a larger τ parameter and a positive delta plot slope.

‘What’ and ‘where’ in the auditory system

Like the visual system, the auditory system distinguishes between the identity and the location of the stimuli detected. Both functional imaging studies in humans and tracing studies investigating cortical connections in non-human primates suggest that the auditory system is organized in parallel and hierarchical pathways specialized for the extraction and processing of spatial and non-spatial auditory information (Gifford and Cohen, 2005; Kaas and Hackett, 1999; Lomber and Malhotra, 2008; Rauschecker and Tian, 2000; Romanski et al., 1999). The lemniscal auditory thalamocortical projection terminates in the core regions of the primary auditory cortex of the temporal lobe. In the non-human primate, serial and parallel processing take place in the surrounding secondary auditory cortices, the ‘belt areas’, bordered laterally by ‘parabelt’ regions (Bizley and Cohen, 2013; Romanski et al., 1999). Romanski and colleagues (Romanski et al., 1999) traced two parallel pathways in the non-human primate brain, that originate in separate cochleotopic auditory fields of the lateral belt area, and terminate in distinct region of the frontal lobes. Based on the specificity of neurons in the lateral belt (Tian et al., 2001) and the functionality of the distinct frontal lobe regions (Romanski et al., 1999), the authors inferred that the pathway originating from the anterolateral section of the belt area and terminating in ventral prefrontal regions specializes in non-spatial auditory processing. The second pathway originates in the caudolateral section of the belt area and terminates in the caudal dorsolateral prefrontal cortex which specializes in localization of sound. The human auditory cortical pathways are organized in a similar parallel manner, with specialized spatial and non-spatial auditory processing networks (see Figure *4*B) (Alain et al., 2001; see for review Arnott et al., 2004; Maeder et al., 2001; Rauschecker and Tian, 2000). A dorsal network which includes the inferior parietal lobe, the superior frontal sulcus and posterior areas of the frontal lobe are involved in spatial auditory processing, spatial working memory, and audiomotor processing (Alain et al., 2001; Arnott et al., 2004; Bizley and Cohen, 2013). The ventral network, which includes the anterior temporal lobe and inferior frontal regions, involves non-spatial auditory-object processing and recognition (Alain et al., 2001; Arnott et al., 2004; Maeder et al., 2001). These pathways are interconnected in a direct and indirect manner (Bizley and Cohen, 2013; Huerta et al., 1987; Rao, 2008).

Relating neural measures of the auditory system with cognitive models

Similar to its visual counterpart, the simultaneous parallel dual-pathway architecture of the auditory system could be qualitatively and quantitatively linked to dual-route model of the Simon effect (De Jong et al., 1994). Yet, one may wonder why some studies provide evidence for negative-going delta plots while others do not. Xiong and Proctor (Xiong and Proctor, 2016) note that the slope of the delta plot is dependent, among other things, on the frequency of the target stimulus. When the target stimulus frequency was below 1000 Hz, the task-irrelevant direct process seems to dissipate (Simon et al., 1976) and a negative slope was measured (Xiong and Proctor, 2016). However, when the experiment was set with frequencies above 1000 Hz (Proctor and Shao, 2010; Wascher et al., 2001), the delta plot was steady with a positive slope.

Why does frequency matter? It is possible that the answer lies in the computational mechanism of localization and tone detection. In general, auditory localization rests on two main computational mechanisms. The physical power of the sound is higher in the ear that is close to the source of the sound, and lower when reaching the far ear. This difference is detected by a process that computes the interaural level differences (Hartmann and Constan, 2002). The other mechanism is the computation of interaural time difference (Zwislocki and Feldman, 1956), which happens because the lateralized sound reaches one ear earlier than the other. Localization is efficient for frequencies below 1000 Hz. As frequencies increase, the time difference needed for accurate localization increases, to the point, above 1500 Hz, that localization is impossible (Brughera et al., 2013). In contrast, tone-recognition is more efficient for higher tones, 1000 Hz and above (Suzuki and Takeshima, 2004). Why should frequency matter to the account of the temporal dynamics of the auditory Simon effect? It is plausible that when high tones (>1000Hz) are presented in the task, the relevant tone-recognition process is more efficient and evidence is accumulated faster. However, the task-irrelevant processing of localization is less efficient. Low frequencies (<1000 Hz) are in the optimal range for the task-irrelevant localization process, while tone-recognition is relatively poor. This implies that in the low frequencies condition, the time-to-peak of the task-irrelevant spatial process will arrive relatively sooner, and for the high frequencies condition, the time-to-peak is later. In terms of the DMC model, a clear and measureable prediction would be that the τ parameter that best fits the distribution of RTs acquired from a high-frequency auditory Simon task is larger than the τ parameter that best fits RTs acquired from a low-frequency auditory Simon task.

‘What’ and ‘where’s in the somatosensory system

Unlike the visual and auditory systems, the somatosensory system processes both internal and external stimuli: the relative position of parts of the body, internal sensations as pain or pressure, and external signals of object in touch with the body (Dijkerman and de Haan, 2007). External objects are localized and their non-spatial characteristics are extracted. However, the evidence for two principal anatomical and functional pathways designate to process spatial and non-spatial somatosensory information are not clear-cut. Reed and colleagues (Reed et al., 2005) demonstrated that primary and secondary somatosensory cortices, the inferior parietal cortex, and the left superior parietal cortex were equally involved in both localization and identification of the sensory objects. The localization of sensory object involves activation in the bilateral superior parietal cortex and the precuneus. The identification of sensory object involved additional activation of the frontal pole, motor cingulate, and right premotor areas. De Santis and colleagues (De Santis et al., 2007) provided an additional angle by examining the temporal dynamics of spatial and non-spatial processing in the somatosensory system, suggesting that the parallel pathways are segregated within 100 ms from signal onset. In an electrophysiological study, Forster and Eimer (Forster and Eimer, 2004) demonstrated that attentional selection to spatial versus non-spatial attributes of vibrotactile stimulation are two independent process, and take place in parallel. Finally, Dijkerman and de Haan (Dijkerman and de Haan, 2007) report an extensive review of studies including patient, functional neuroimaging, and neurophysiology data. They propose a comprehensive model describing two dissociable cortical processing streams in the somatosensory system; one for the immediate guidance of action, and one for conscious perception and memory (see Figure *4*C). The model postulates that both processing streams emerge from a common source in the thalamus projecting to the anterior parietal cortex (APC, also referred to as the primary somatosensory cortex). The spatial action-oriented pathway projects from the APC to the secondary somatosensory cortex (SII) and further to the posterior parietal cortex. The non-spatial perceptual pathway projects from the APC to the SII and further to the insula. Dijkerman and de Haan (Dijkerman and de Haan, 2007) noted that although the model resembles the visual and auditory counterparts, crucial differences must be noted. First, the model distinguishes between body internal- and external stimuli. Second, the pathways are not as independent as the pathways of the visual system.

Relating neural measures of the somatosensory system with cognitive models

So far, a non-negative delta plot slope is a consistent finding in somatosensory Simon studies (Salzer, 2013; Salzer et al., 2014). This might imply, based on the DMC, that the task-irrelevant direct route processing spatial attribute of the stimuli is slower to propagate and dissipate, relative to visual and auditory modalities. However, a negative slope was acquired when a centrally positioned vibrotactor was added (Exp. 3 in Salzer et al., 2014). In retrospect, the authors suggested that the additional central condition was a non-corresponding condition, decreasing the frequency of corresponding trials. As a result, participants updated their strategy accordingly, by enhancing the suppression of the task-irrelevant direct route. Somatosensory Simon studies are fewer by orders of magnitude relative to the visual and auditory counterparts (Hasbroucq and Guiard, 1992; Medina et al., 2014; Salzer et al., 2014). Consequently, more research is needed to better understand the factors affecting the temporal dynamics of the somatosensory Simon effect. It would be interesting to compare visual and tactile Simon tasks, the onset time of partial errors EMG with respect to parameter τ and the slope of last quantile of the delta slopes, in the DMC framework.

Interim summary

In general, for all three modalities, the literature points toward two distinct pathways for the spatial action-oriented aspect of the stimulus, and its non-spatial identity. This neuroanatomical architecture elegantly mimics the dominant dual-pathway architecture from the cognitive literature. Furthermore, closer inspection of the literature suggests that the processing speed of the two pathways can be modulated by the nature and complexity of the stimulus, as well as by attention and strategies depending on task context. The DMC might help us to understand these effects in more detail, as corresponding changes in model parameters, in particular the parameter that determines the speed and duration of the automatic process, influences the decision.

The model-based cognitive neuroscience approach can be used to test many of the predictions laid out above. For example, stronger neural representations in the ‘what’ and ‘where’ pathway should have an effect only on specific DMC parameters: the mean drift rate of the controlled process and the amplitude or time-to-peak of the automatic process, respectively. Recent developments in neuroimaging analysis techniques, such as multivariate pattern analysis techniques (MVPA; Haxby et al., 2001; Kriegeskorte et al., 2008; Norman et al., 2006) and encoding models (van Gerven, 2016), allow us to look into the strength of such representations. The cognitive model-of-choice is crucial to this approach, as it can efficiently identify parameters-of-interest for individual subjects. If the model is unable to do so, the estimated parameters will not properly capture individual variability and their relationship to neural signals become meaningless. For now, it remains to be seen whether DMC parameters can easily be identified, and further validation is needed.

Who controls the ‘what’ and ‘where’ pathways

Information is processed in the ‘what’ and ‘where’ pathways in a parallel manner leading to a response conflict in the non-corresponding condition. How does the decision to respond based on the ‘what’ pathway and ignore or suppress the ‘where’ pathway come about in the brain? The spatial ‘where’ pathway plays a role in guiding one’s actions (visual: Kravitz et al., 2010; auditory: Warren et al., 2005; tactile: Dijkerman and de Haan, 2007). On a portion of the trials, Servant and colleagues (Servant et al., 2016) measured incorrect EMG prior to the onset of the correct response, supporting the notion that spatial location of the target stimulus guides the automatic irrelevant response. The right inferior frontal cortex (IFC) and the basal ganglia are thought to play a crucial role in inhibiting an already initiated manual response: the IFC projects to the subthalamic nucleus (STN), an important basal ganglia input node, in an excitatory manner. The STN, in turn, excites the globus pallidus (GP), another basal ganglia node. The GP inhibits the thalamus, which results in “slamming the brakes” on the response processed by the motor cortex (Aron and Poldrack, 2006). Forstmann and colleagues (Forstmann et al., 2008b) found that the activity of the right inferior frontal gyrus (rIFG) was correlated with the negativity of the delta plot slope, associated with strength of suppression of the task-irrelevant direct route. Although the right IFC is thought to play a common inhibitory function in the suppression of motor responses, as well as the control of thoughts and attentional resources, the generality of the fronto-subthalamic inhibitory circuitry remains to be established (for discussion see Aron, 2007; Aron et al., 2016; Hampshire et al., 2010).

We think it will be interesting for future work to explore how inter- and intra-individual variability of the latent variables in the DMC is related to neural activity during task performance (Turner et al., 2015, 2013). Importantly, such an approach could help distinguish between qualitative accounts of the mechanisms underlying the Simon task. For example, if frontal areas are involved in active selective suppression of the irrelevant response during incongruent trials (Ridderinkhof, 2002), one would expect shared variance between individual differences in the duration of the automatic response (as estimated by the DMC parameter τ) and activity in frontal regions, such as the IFG, as well as cortico-basal ganglia connectivity measures. In contrast, if the observed behavioral patterns are simply the result of the passive decay of automatic process (Hommel, 1994), one would expect to find such a relationship between the duration of the automatic process on the neural activity in early sensory areas.

Concluding remarks

In the present review we proposed a comprehensive framework to account for the temporal dynamics of the Simon effect as measured by different variants of the Simon task. The framework brought forth in the present review links cognitive models with the neuronal pathways accountable for the processing of spatial (‘where’) and non-spatial (‘what’) information. Recent literature suggests that this organization is common among vision, audition, and somatosensory modalities. We have argued that various factors such as modality and complexity of the incoming information, task settings, and attentional biases determine the propagation of the signals through the pathways. We reasoned that a model-based cognitive neuroscience approach can help to parsimoniously incorporate a multiplicity of complex and conflicting data from the same, or similar tasks in different modalities. Finally, we provided examples of how the linking of behavioral and neural data could be used to test this framework. While further work must be done, we believe that the use of mathematical cognitive models such as the DMC construct the bridge between behavioral and neural data to finally provide comprehensive account to the temporal dynamics of the Simon effect.

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Figures

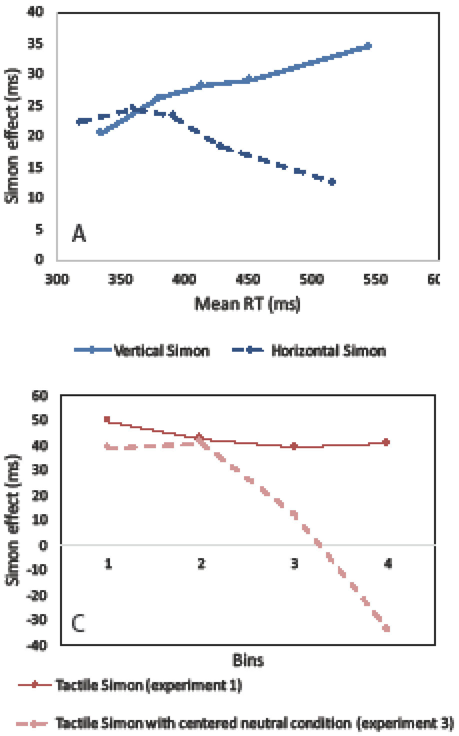

Figure 1 - Distribution of mean Simon effect, also known as delta plots, for (A) horizontal and vertical visual Simon task (data adapted with permission from Töbel et al., 2014), (B) high- and low-frequency auditory Simon task (data adapted with permission from Xiong and Proctor, 2016), and (C) tactile Simon task with- and without-central neutral condition (data adapted with permission from Salzer et al., 2014).

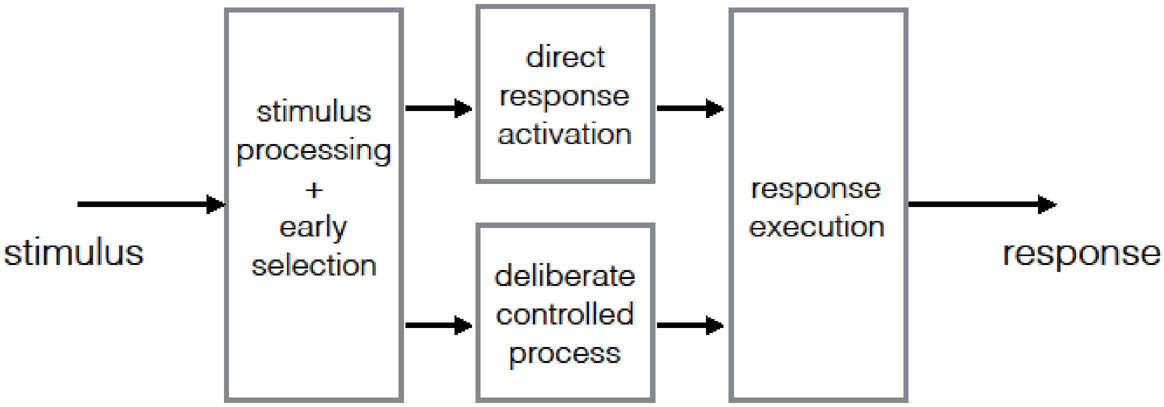

Figure 2 - Elementary architecture of the dual-route model based on the proposal by De Jong et al., 1994. The *deliberate controlled process* corresponds to the task-relevant indirect route, whereas the *direct response activation* corresponds to the task-irrelevant direct route.

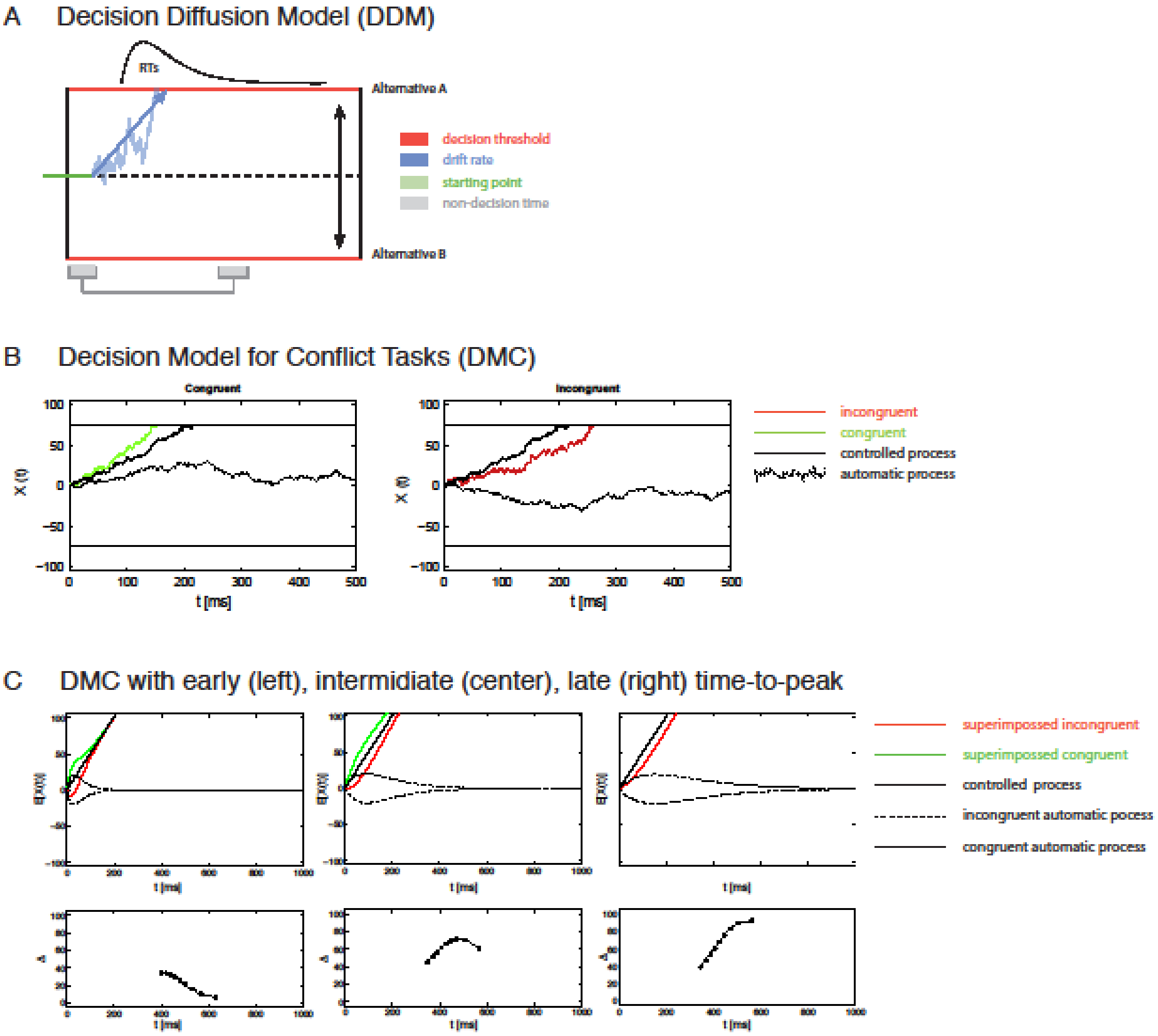

Figure 3 - (A) Diffusion Decision Model (reconstructed with permission from Mulder et al., 2014). The random walk process, captured by the drift rate (blue), represents the difference in evidence for the two-response alternative. As soon as the random walk hits one of the two thresholds (red) a decision is made. Decision time is the time required to reach a boundary. Non-

decision time is the time required for additional, non-decision-related processes (gray). The Diffusion Model for Conflict tasks (DMC) is shown in (B) and (C). (B) A sample of the trajectories of the activation of control (dark gray) and automatic (light gray) processes in a single congruent (left) and incongruent (right) trial. The green (congruent) and red (incongruent) lines depict the superimposed processes. (C) The upper panel presents the mean activation functions. Solid black line - controlled activation; dotted black line - congruent automatic activation; dashed black line - incongruent automatic activation; solid colored lines - the superimposed activation in the congruent (green) and the incongruent (red) condition. The lower panel represent the delta plots for early, intermediate, and late time-to-peak (B and C were reconstructed with permission from Ulrich et al., 2015).

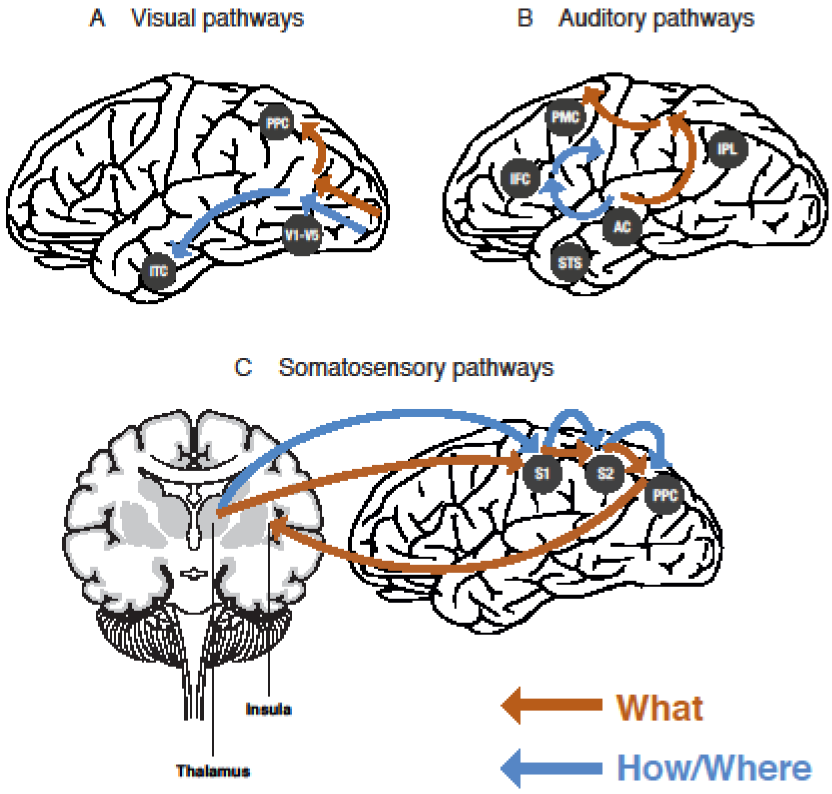

Figure 4 - Framework of ‘what’ (brown) and ‘how/where’ (blue) pathways in the (A) visual (Milne and Goodale, 1995), (B) auditory (Bizley and Cohen, 2013), and (C) somatosensory (Dijkerman and de Haan, 2007) networks.