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Striatal activation reflects urgency in perceptual decision making

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ABSTRACT

Deciding between multiple courses of action often entails an increasing need to do *something* as time passes - a sense of urgency. This notion of urgency is not incorporated in standard theories of speeded decision making that assume information is accumulated until a critical fixed threshold is reached. Yet, it is hypothesized in novel theoretical models of decision making. In two experiments, we investigated the behavioral and neural evidence for an "urgency signal" in human perceptual decision making. Experiment 1 found that as the duration of the decision making process increased, participants made a choice based on less evidence for the selected option. Experiment 2 replicated this finding, and additionally found that variability in this effect across participants covaried with activation in the striatum. We conclude that individual differences in susceptibility to urgency are reflected by striatal activation. By dynamically updating a response threshold, the striatum is involved in signaling urgency in humans.

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Introduction

Timing is extremely important when making decisions. This is especially clear, for example, when driving in traffic: as you move closer to the car in front of you, there is increasing pressure to hit the brakes or switch lanes and overtake. The importance of this notion of *urgency* has only recently been acknowledged in theoretical models of decision making (Cisek et al., 2009; Deneve, 2012; Ditterich, 2006a, 2006b; Drugowitsch et al., 2012; Frazier and Yu, 2008; Hanks et al., 2014; Ratcliff and Frank, 2012; Thura et al., 2012).

Decision making is thought to involve a gradual accumulation of evidence in favor of various courses of action (Forstmann et al., 2016; Gold and Shadlen, 2007; Mulder et al., 2014). This accumulation process continues until it crosses a response threshold - the quantity of evidence required to trigger a decision - resulting in selection of a single course of action. Conventional models of the decision making process have long assumed that these thresholds are fixed, meaning that the amount of evidence required to trigger a decision does not change during the course of a single decision (Brown and Heathcote, 2008; Ratcliff, 1978; Usher and McClelland, 2001; Vickers, 1979). In contrast, recent models have argued for a dynamic adjustment of the threshold within single decisions to account for the effects or urgency (Bowman et al., 2012; Churchland et al., 2008; Cisek et al., 2009; Ditterich, 2006a, 2006b; Drugowitsch et al., 2012; Hanks et al., 2014; Hawkins et al., 2015; Ratcliff and Frank, 2012; Thura et al., 2012).

A series of animal studies have given support for the notion that the basal ganglia, and in particular the striatum, are involved in decision urgency. Striatal activation appears to play a critical role in the execution of actions (Chevalier et al., 1985; Deniau and Chevalier, 1985), and in particular motor actions (Turner and Desmurget, 2010). The basal ganglia has been proposed to be involved in the regulation of thresholds within single decisions (Thura and Cisek, 2016; Thura et al., 2014). In these studies, monkeys performing expanded judgment tasks (Busemeyer and Rapoport, 1988; Irwin et al., 1956; Vickers, 1979) became faster and less accurate, and had more vigorous response movements, when decision urgency was induced. Based on this, these authors proposed that basal ganglia plays a central role in decision urgency (see also Choi et al., 2014; Haith et al., 2012).

Additionally, the role of striatum in the context of explicit speed-accuracy tradeoffs in perceptual decision making in humans has been extensively documented (Forstmann et al., 2008; Ivanoff et al., 2008; Van Maanen et al., 2011; Van Veen et al., 2008; Winkel et al., 2012). For instance, the difference in the striatal BOLD signal between speed-stressed and accuracy-stressed trials correlates with differences in the response threshold parameter, both in terms of across-participant variability (Forstmann et al., 2008) and across-trial variability (Van Maanen et al., 2011). However, the neural mechanisms that are involved in within-trial threshold adjustment in human perceptual decision making are largely unknown (but see Gluth et al., 2012, for a related study in value-based decision making). Here, we hypothesize that striatal activation additionally regulates the speed of responding *during* a decision to accommodate a sense of urgency in humans.

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In this paper, we first verified that people will decrease the quantity of evidence they are willing to accept as the time required to make a decision increases (Experiment 1), following the predictions of recent decision making models (Cisek et al., 2009; Thura et al., 2012). To increase the average decision time, we experimentally manipulated the speed with which the stimulus appeared on the screen. Secondly, we tested whether the striatum is involved in adjusting the amount of evidence required *during* a trial (Experiment 2). Specifically, we hypothesized that an increased sense of within-trial urgency observed in behavioral data would be reflected in increased activation in the striatum. Moreover, although Experiment 1 was a pure behavioral study and Experiment 2 was conducted while participants were undergoing fMRI we expect the behavioral results to replicate.

Materials and methods

Participants

Twenty-five participants (fourteen female, mean age: 22; SD: 2.5) participated in Experiment 1 for research credit or monetary compensation. A separate group of twenty participants (eleven female; mean age: 24; SD: 7) participated in Experiment 2, also for research credit or monetary compensation. The University of Amsterdam Ethics Committee approved the studies and all participants gave informed consent prior to participation in the experiments. All participants had normal or corrected-to-normal vision. In Experiment 1, two participants were excluded for failure to follow task instructions. In Experiment 2, one participant was excluded from the behavioral and fMRI analyses because they did not complete the experiment. Three further participants were removed from the fMRI analyses: one due to excessive head motion and two due to excessive noise in the data.

Behavioral paradigm

In both experiments, participants made decisions between two options (henceforth "stacks") that grew taller at different rates, by accumulating increments of height (henceforth "bricks") at discrete time steps (Fig. 1; cf. Brown et al., 2009; Hawkins et al., 2012a). At the beginning of each trial, a fixation cross was presented in the middle of the screen. Next, the stimulus onset was indicated by displaying an initial brick for each stack, and the stimulus was built up on the screen in discrete time steps that were separated by an experimentally manipulated delay period (the "drop delay"). At each time step, there was 80% chance for a brick to fall onto one stack, and 60% chance for a brick to fall onto the other stack; we refer to these values as the "drop rate" for the target and distractor stacks, respectively. There was a maximum of 25 time steps per trial and trials ended as soon as a response was given or the maximum number of time steps was reached. The order of delays was randomized to have a fully mixed experimental design. Participants were instructed to press a button (left or right) with their index finger to indicate the stack with the higher drop rate as quickly as possible. Since the difference in accumulation rate between the correct and incorrect stacks was the same in each experimental condition, task difficulty – operationalized as the difference in accumulation rates – was not manipulated; only the overall speed of the task was manipulated. The location of the correct stack was randomized across trials to ensure that participants would not be biased to choose the left or right response.

Experiment 1 comprised five drop delay conditions: 200 ms, 400 ms, 600 ms, 800 ms, or 1000 ms. Each condition consisted of 100 trials for a total of 500 trials. Participants indicated their response with the "z" and "m" keys on a standard PC keyboard. Accuracy feedback was provided for 200 ms.

Experiment 2 comprised two delay conditions (200 ms and 400 ms), with 90 trials per condition and 20 null trials in which a fixation cross was presented for the duration of the trial. The experiment was split in two blocks of 100 trials with a brief break in between, during which a new scan sequence was started. Each trial started with a variable jitter (either 0 ms, 500 ms, 1000 ms, or 1500 ms), followed by a fixation cross (200 ms). Participants indicated their response by pressing a button box with either a left or right index finger. Once a response was given, bricks continued to accrue at the same pace until 25 time steps had elapsed, and feedback appeared for 200 ms. A new trial started every 12th second from the beginning of the scan sequence.

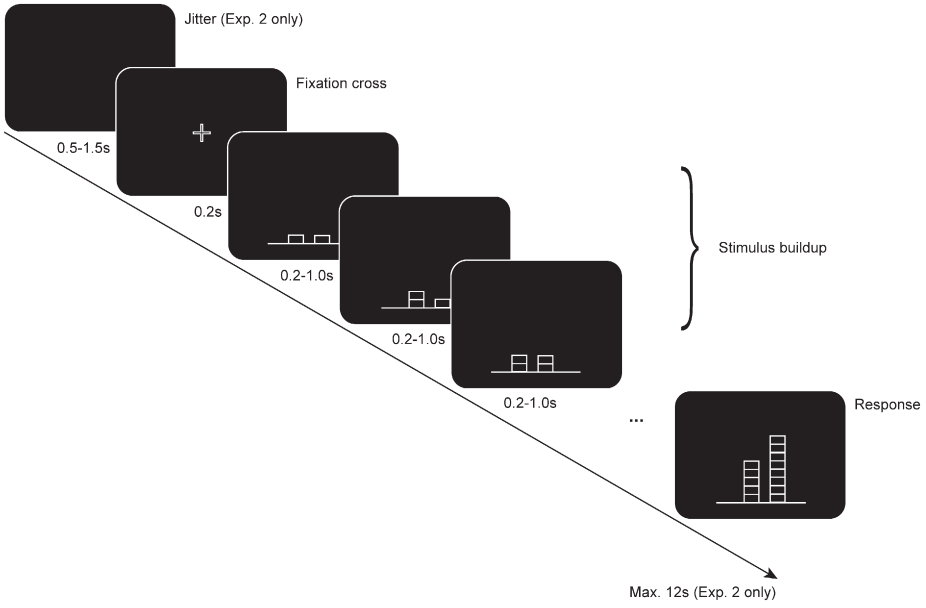

Fig. 1. Experimental paradigm for Experiments 1 and 2. On each trial, bricks fell on the left and right stack with different rates. Participants were instructed to evaluate the stimulus buildup to infer the stack with the greater rate, and press a response button with the right or left index finger.

A difficult element of the task is the balance between speed and accuracy: when only a few bricks have accumulated – early in the process – the distractor (i.e., incorrect) stack may be taller than the target by chance. Thus, the decision maker has to infer the probability of a chance difference in stack height to avoid incorrect choices. This paradigm allowed us to develop a cognitive model that quantifies the exact amount of evidence supporting each choice, because all information pertaining to the decision remained on screen at all times (Brown et al., 2009; Busemeyer and Rapoport, 1988; Cisek et al., 2009; Hawkins et al., 2012b, 2012c; Irwin et al., 1956; Kira et al., 2015; Vickers, 1979).

Cognitive modeling of the evidence accumulation process

We developed a Bayesian model of decision making to quantify the level of evidence for a choice at the moment of the decision. This model, referred to as the Rate Difference model, takes into account knowledge about the distribution from which the presented evidence is sampled at each time step, and knowledge about the height of the two stacks at each time step. The model assumes that this information is used to compute the probability that one stack accumulates bricks faster than the other. This proposal is related to the Ideal Observer model (e.g., Brown et al., 2009; Kira et al., 2015; Van Maanen et al., 2012a, see also Inline Supplementary Methods 1). However, the two models differ in their assumptions about what the decision maker knows about the environment. The Ideal Observer model computes the probability that the chosen stack is the target, given that the rates of the distractor and the target are known (i.e., the probability that a brick will fall at each time step, for the target and distractor stacks). The Rate Difference model relaxes the assumption that participants have precise knowledge of the rates of the two stacks, and computes the probability that one stack accumulates bricks faster than the other.

During the task, participants must decide which of the two stacks accumulates faster. Bricks fall on the two stacks following two independent binomial distributions with rates $\theta_t = 0.8$ (i.e., the drop rate for the target stack) and $\theta_d = 0.6$ (distractor stack). Participants were not informed about the two rates. The uncertainty around the two rates at the beginning of the trial is quantified as $\theta_t \sim Beta(1,1)$ and $\theta_d \sim Beta(1,1)$. Therefore, after n time steps:

$$\theta_t \sim \text{Beta}(1 + s_t, 1 + f_t)$$

$$\theta_d \sim \text{Beta}(1 + s_d, 1 + f_d)$$

$$\delta = \theta_t - \theta_d$$

where θ_t is the posterior distribution of the rate of the target stack, which follows a beta distribution with parameters $\alpha = 1 + s_t$ (s_t being the number of bricks that fell on the target stack) and $\beta = 1 + f_t$ (with $f_t = n - s_t$, i.e., the number of time steps where a brick did not fall on the target stack). θ_d is the posterior distribution of the rate of the distractor stack, which follows a beta distribution with parameters $\alpha = 1 + s_d$ (s_d being the number of bricks that fell on the distractor stack) and $\beta = 1 + f_d$ (with $f_d = n - s_d$). The variable δ is the difference between the two rate distributions after n time steps. The probability of δ being positive (i.e., the probability that θ_t is larger than θ_d, which we refer to as the *evidence*) can be computed as the area underlying the posterior distribution of δ for $\delta > 0$ (Fig. 2).

In the results reported here we focus on the Rate Difference model. However, for Experiment 1 we developed and compared three models (see Inline Supplementary Methods 1) and subsequently selected the Rate Difference model to apply in Experiment 2. This setup ensured that the degrees of freedom that are introduced when developing cognitive models were constrained by the data of Experiment 1. The application of the selected model to Experiment 2 therefore did not depend on model adjustments that were driven by the data of Experiment 2. As a result, there is less room for researcher bias in interpreting the notion of evidence predicted by the cognitive model.

Estimation of the non-decision time

Because there is a time lag between decision and response execution, a decision may be made for the largest stack but the display may (or may not) change in the moments before the button is pressed. To correct for this, we assumed (following Brown et al., 2009) that participants aimed to choose the largest stack in the display. Under this

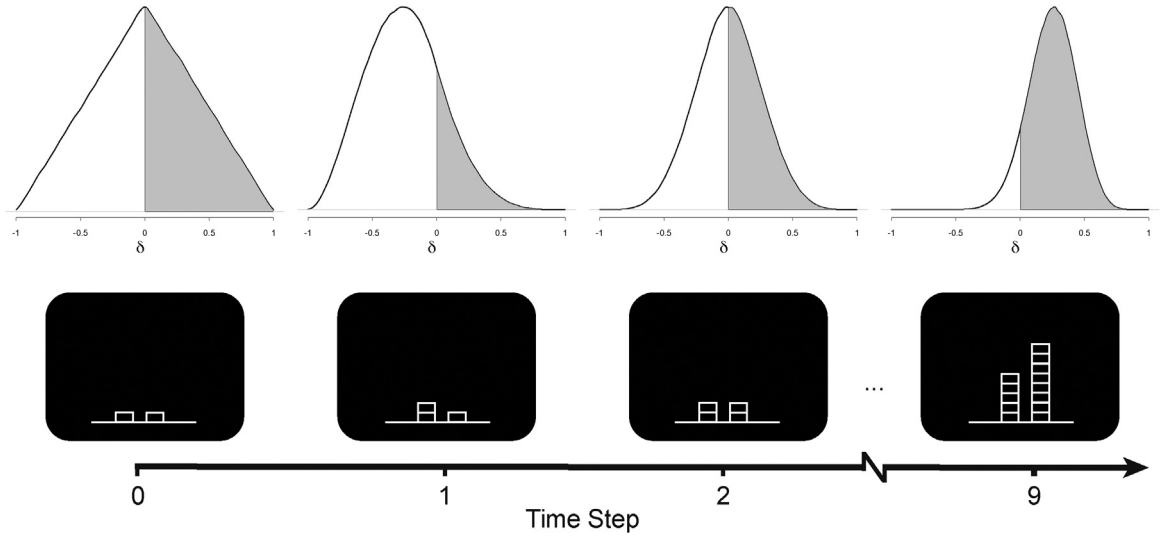

Fig. 2. Illustration of the evolution of evidence for a response in the Rate Difference model. The white and gray areas represent the evidence in favor of a left and right response, respectively. As time progresses and the stacks accumulate bricks, the posterior distribution of the rate difference (δ) changes, and so does the evidence for the left and right responses.

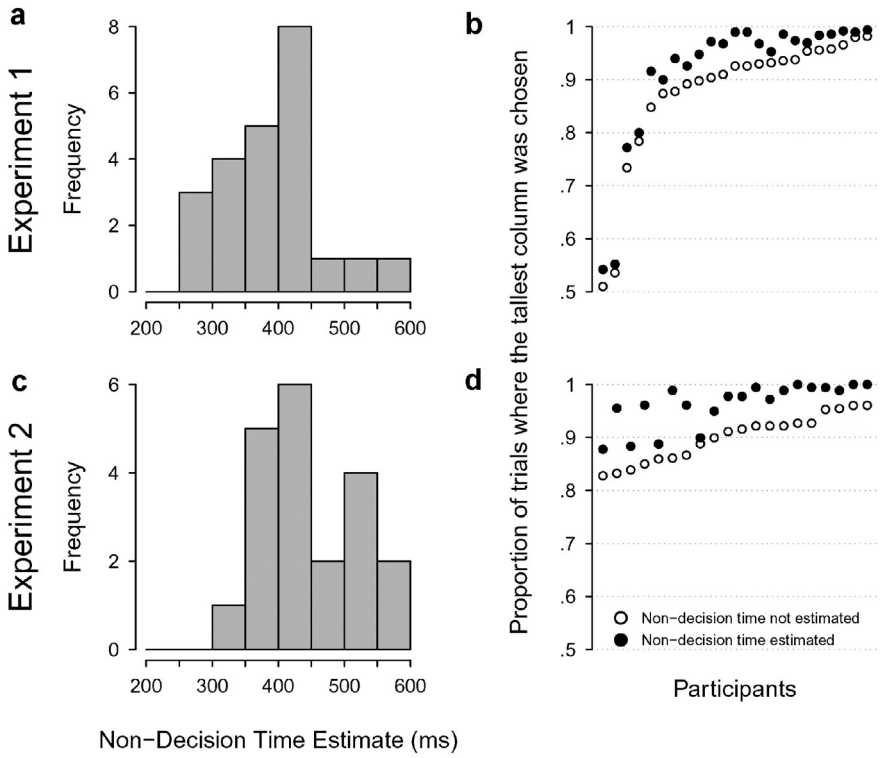

Fig. 3. Estimate of non-decision time (t_0) for Experiments 1 and 2. (a) The distribution of t_0 across participants in Experiment 1. (b) For each participant in Experiment 1, the proportion of trials where they chose the largest stack without taking into account the t_0 estimate (open symbols) and when taking into account a t_0 estimate (filled symbols). For all participants this proportion is largest for the filled symbols. (c) The distribution of t_0 across participants in Experiment 2. (d) The proportion of trials where participants chose the largest stack in Experiment 2, both corrected and uncorrected for t_0.

assumption we can estimate the time lag (non-decision time or t_0) by considering the state of the display at RT - t_0. Per participant, we maximized the proportion of trials where the participant chose the largest stack by estimating t_0 using a simple root finding algorithm. For each participant, we searched a range of non-decision times [0–600 ms] for the value that gave the highest proportion of trials on which the participant chose the largest stack. If a range of t_0 estimates led to the same proportion, we took the midpoint of the range. The estimates of t_0 are generally higher in Experiment 2 (which was conducted in the MRI scanner bore, Fig. 3). This is consistent with previous findings (Koch et al., 2003; Van Maanen et al., 2016).

Statistical analyses

We used Bayesian ANOVA (Rouder et al., 2012) to quantify the effect of the drop delay manipulation on behavioral performance. That is, we compared the likelihood of a statistical model that included the different drop delay levels as a factor against the likelihood of a statistical model with only random participant intercepts. The likelihood ratio of these models (the Bayes factor, BF) indicates how much more likely the data are under the more complex statistical model compared to the simpler (baseline) statistical model. We report exact BFs, unless the BF is considered "decisive" according to Jeffreys' (1961) scale (BF > 100).

Regression of time step on evidence

We regressed the probability that the chosen alternative was correct (i.e., the evidence) as defined by the Rate Difference model against response times (RT), for every trial of each participant and condition. Although a linear decrease in evidence as a function of decision time may be a simplification (Drugowitsch et al., 2012; Hawkins et al., 2015; Zhang et al., 2015), it was the simplest assumption given the sparsity of the data. For the behavioral analyses, we used a linear-mixed effects model (Baayen et al., 2008) in which the level of evidence was the dependent variable, and drop delay condition and time step (on a trial-by-trial basis) were the independent variables. We included separate intercepts for each participant. Statistical significance of the estimated regression weights was assessed using Monte Carlo simulations. *p*-values were computed using Satterthwaite's approximation of the denominator degrees of freedom.

Table 1
Model comparison for Experiment 1.

Model	Degrees of freedom	AIC	BIC	χ^2	*p*
0	7	−15,126	−15,074		
1	8	−16,031	−15,973	907.8	<0.001
2	12	−16,035	−16,947	11.45	0.022

Table 2
Model comparison for Experiment 2.

Model	Degrees of freedom	AIC	BIC	χ^2	*p*
0	4	−4902.9	−4878.2		
1	5	−5497.8	−5467.0	596.9	<0.001
2	6	−5495.9	−5458.8	0.068	0.79

We fitted and compared three linear mixed-effects models to the data of Experiments 1 and 2. Model 2 included the time step at the time of decision, the condition (drop delay), and the interaction between those; Model 1 simplified Model 2 by excluding a main effect of condition and the interaction between condition and time step. Model 0 was a base-line model that only included the condition, and not the time step. Tables 1 and 2 show a model comparison using AIC, BIC, and χ^2-difference tests. AIC and BIC indicate how well a model balances goodness-of-fit with model complexity, with lower values indicative of the better model (Akaike, 1974; Schwarz, 1978). A χ^2-difference test of two models of increasing complexity indicates whether including the additional degrees of freedom is warranted given the likelihood ratio of the models. For both experiments, inclusion of time step as a factor was warranted as shown by lower AIC and BIC values for Models 1 and 2 as compared to the base-line Model 0, as well as a significant χ^2 statistic of the likelihood ratio of Model 0 and Model 1. In Experiment 1, the main effect of condition was warranted, as shown by lower AIC and BIC values for Model 2 as compared to Model 1, and a significant result for the χ^2-difference test. For Experiment 2, this was not the case, and the simpler Model 1 was preferred by all three measures.

fMRI data acquisition and analysis

Imaging data were acquired in two scan sessions (one for each block of Experiment 2) using a Philips 3T Achieva scanner. At the beginning of the experiment, T1 anatomical scans were acquired for each participant (220 slices; TR: 8.2 s; TE: 3.8 ms; flip angle: 8°; FOV: 240 mm; voxel size: $1 \times 1 \times 1$ mm). For functional imaging, echo-planar images (EPI) scans were acquired in transverse orientation (slice thickness: 3 mm; 37 slices; TR: 2 s; TE: 27.63 ms; flip angle: 76.1°; FOV: 240 mm; voxel size: $3 \times 3 \times 3$ mm). To monitor fixation of participants during the experiment, we used an Eyelink II system operating at a sampling rate of 1000 Hz.

fMRI analyses were performed using FEAT (FMRI Expert Analysis Tool), version 6.00, part of FSL (FMRIB Software Library, www.fmrib.ox.ac.uk/fsl). Images were realigned to correct for small head movements using MCFLIRT motion correction (Jenkinson et al., 2002). Data were spatially smoothed using a 5 mm FWHM Gaussian kernel, temporally filtered using a nonlinear high-pass filter (100 s cutoff), and pre-whitened. All functional images were registered using the participants' individual high-resolution anatomical images acquired at the beginning of the experiment and normalized into MNI space by linear scaling.

First and second-level analyses were performed to identify decision-related BOLD activity in the whole brain. A third-level analysis identified which decision-related areas correlated with a behavioral measure of urgency, separately for the two drop-delay conditions. Finally, a conjunction analysis (Nichols et al., 2005) identified which urgency-correlated areas were common across the two conditions. This way, the results are not dependent on the difference in stimulus durations between the two conditions.

In the first level analyses, the design matrix was convolved using a double gamma hemodynamic response function (HRF) and its temporal derivative. A total of five regressors were included: left and right responses, first and second condition (200 and 400 ms), stimulus locked, with a duration equal to the RT (Grinband et al., 2008), and null events. Contrasts were 200 ms vs. baseline and 400 ms vs. baseline. Analyses were completed separately for each participant, for each block. In the second-level analyses, the resulting images for each participant in the two first-level blocks were combined without correcting for multiple comparisons. In the third-level analyses, the resulting images across

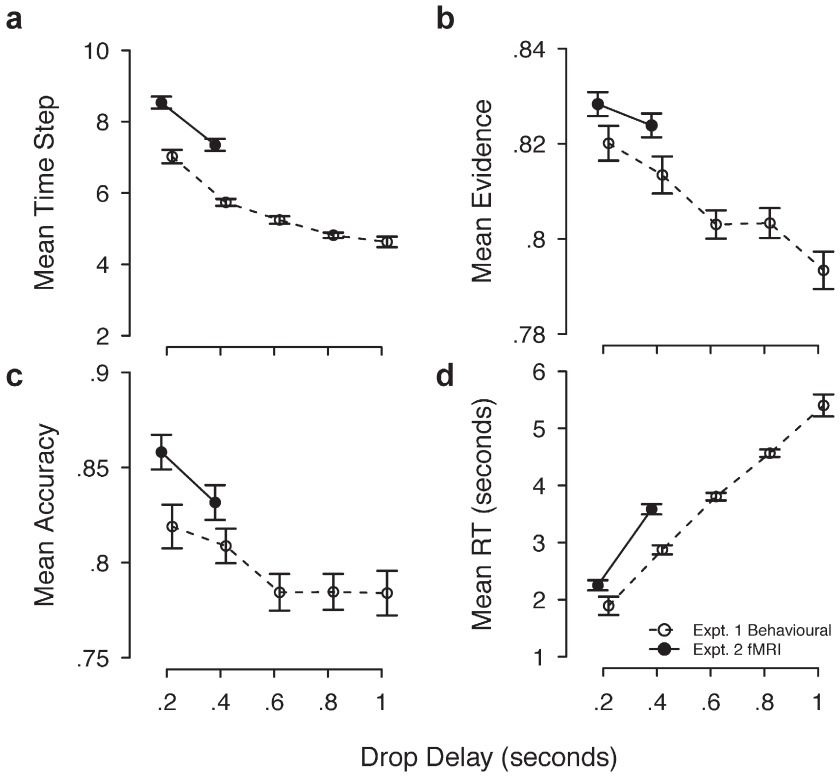

Fig. 4. Behavioral results for Experiments 1 and 2. (a) Mean number of time steps required for a decision per drop delay condition; (b) Mean evidence per drop delay condition, as calculated from the Rate Difference model; (c) Mean accuracy per drop delay condition; (d) Mean response time per drop delay condition. Error bars indicate within-subjects standard error of the mean.

all participants were combined and regressed against the individual participant's regression coefficient of evidence against decision time. Finally, the conjunction analysis was performed to test the overlap of common regions activated in both the 200 ms and 400 ms condition (i.e., areas positively and negatively correlated with the individual slope estimates). Results are reported at a cluster corrected threshold of $z = 2.3$ ($p = 0.05$, using Gaussian random field theory).

Robustness check for correlation of the BOLD signal in the striatum and the evidence coefficients

To ensure that the correlation of the BOLD signal in the striatum and the evidence coefficients is robust against perturbations of the data, we resampled the data with replacement 10,000 times and recomputed regression coefficients. The *evidence coefficient* is here defined as the slope estimate of the regression of the evidence (according to the Rate Difference model) against RT.

Results

Experiment 1

We found that as the drop delay increased, there was a corresponding decrease in the number of discrete steps that elapsed prior to decision (Fig. 4a, BF > 100). This finding suggests that when bricks accumulated more slowly – that is, when there was a larger amount of time between successive evidence increments – participants based their decisions on less stimulus information, consistent with the idea of decision urgency.

To confirm that the effect of drop delay on time step corresponded to a reduction in the evidence used to trigger decisions, we computed an explicit measure of evidence that was derived on an individual trial basis and separately for every participant. We define the *evidence* for a response as the probability that the chosen stack was correct, using the Rate Difference model (see Materials and methods, Section 2.3. Cognitive modeling of the evidence accumulation process). As expected, the average evidence in the display at the time of decision decreased as a function of the drop delay (Fig. 4b, BF > 100). However, this reduction in mean evidence was not associated with a reliable reduction in response accuracy (Fig. 4c, BF = 1.1). Since the drop delay manipulation directly influenced how quickly the stacks grew, mean RT also increased (Fig. 4d, BF > 100).

For most participants in most conditions, the evidence for the chosen alternative decreased as decision times increased, as indicated by the coefficient of a linear regression (Fig. 5a–e shows individual-participant regression lines). Fig. 5f summarizes this finding across participants, showing that the probability of being correct at the time of

Table 3
Beta estimates for the linear mixed-effects model of Experiment 1.

Factor	Estimate	Degrees of freedom	t	p
Intercept	0.86	3400	87.50	<0.001
Time step	−0.0064	10,930	−11.96	<0.001
400 ms	0.0045	10,930	0.72	0.47
600 ms	−0.0060	10,930	−0.96	0.33
800 ms	−0.0024	10,930	−0.39	0.70
1000 ms	−0.015	10,930	−2.42	0.015
Time step × 400 ms	−0.0033	10,930	−4.03	<0.001
Time step × 600 ms	−0.0041	10,930	−4.76	<0.001
Time step × 800 ms	−0.0057	10,930	−6.21	<0.001
Time step × 1000 ms	−0.0057	10,930	−6.29	<0.001

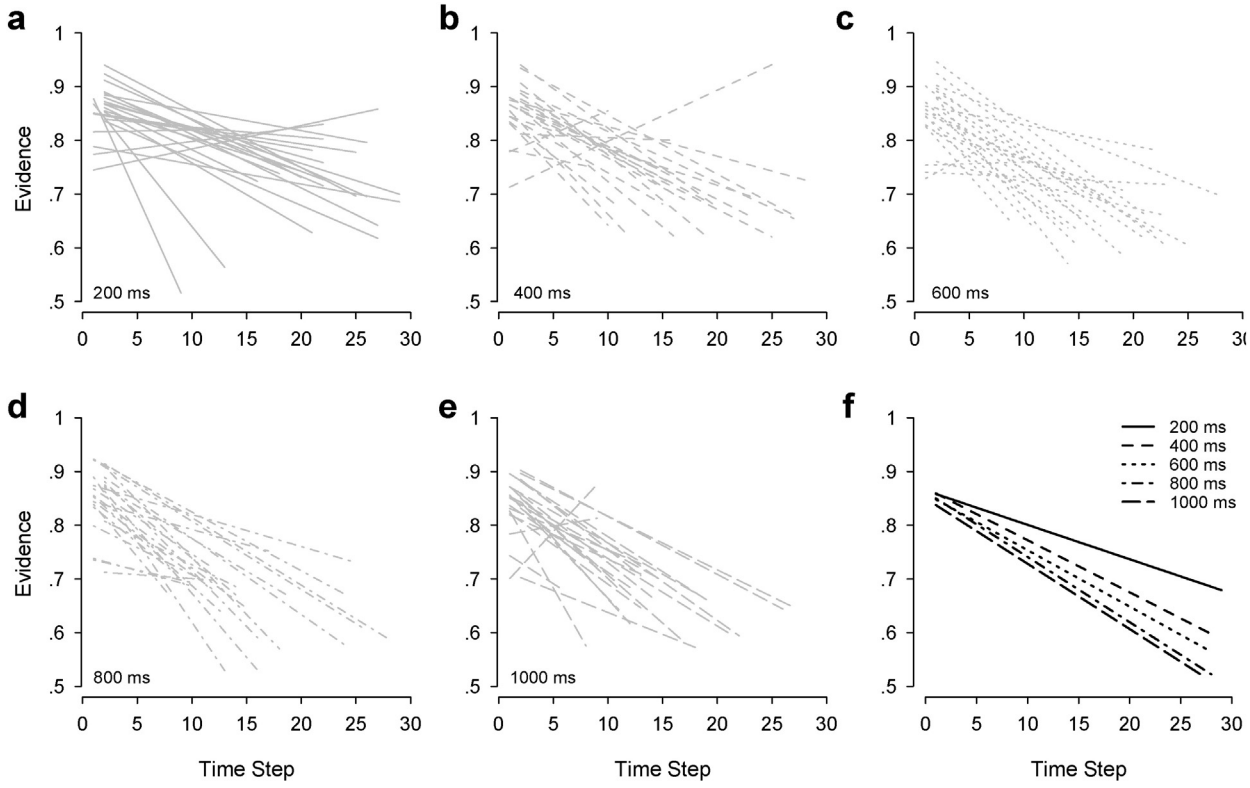

Fig. 5. Individual differences in urgency in Experiment 1. (a–e) Individual regression lines per condition, where the value in the lower left of each panel indicates the drop delay. (f) Regression lines per condition as estimated by a linear mixed-effects model (see Materials and methods for details).

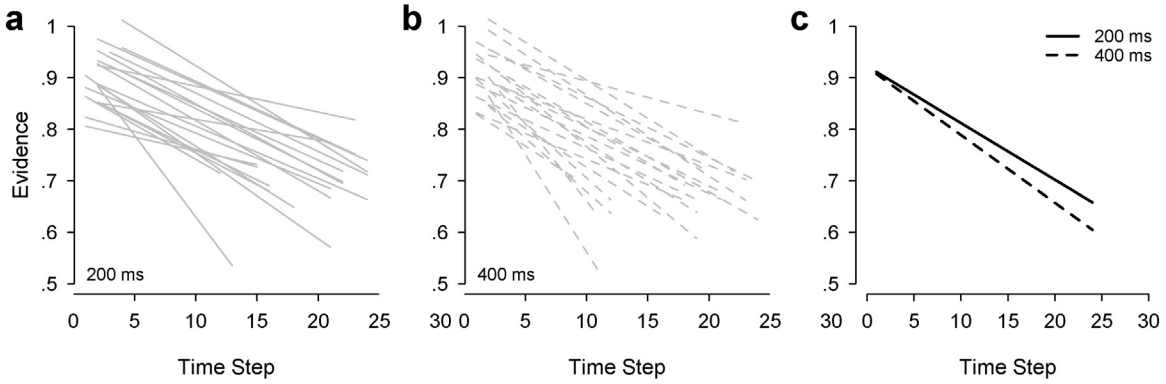

Fig. 6. Individual differences in urgency in Experiment 2. (a–b) Individual regression lines per condition. (c) Regression lines per condition as estimated by a linear mixed-effects model (see Materials and methods, Section 2.6. Regression of time step on evidence for details).

choice was negatively correlated with the number of time steps required for a decision (Table 3 shows the β-weights of the best model for Experiment 1, together with a t-statistic that represents the probability of finding such a weight distribution if the true model did not include that factor, Bates, 2005). Thus, the amount of evidence required to make a decision decreased with elapsed decision time, and this effect was stronger for longer intervals between consecutive time steps.

To support our hypothesis that the effect of urgency is not driven by differences in RT induced by the experimental manipulation (i.e., the drop delays), we additionally fit a regression model in which the individual regression coefficient was predicted by each participant's mean RT per condition. The likelihood of this statistical model under the data was compared against a model that only included the drop delays. We found a Bayes factor of 0.19, indicating that the simpler model without mean RT as a factor is 5.3 times more likely than the more complex model with RT as a factor. Therefore, it is unlikely that the urgency effects observed in behavior were due to differences in RT induced by the drop delays.

Experiment 2

Consistent with Experiment 1, the analysis of behavioral data from Experiment 2 also supported the decision urgency hypothesis (Fig. 4, Mean time step: BF > 100; Mean evidence: BF = 0.55; Mean accuracy: BF = 1.4; Mean RT: BF > 100). Also, as in Experiment 1, as the number of time steps grew larger people were willing to make decisions on the basis of less evidence (Fig. 6 and Table 4). The regression analysis did not support a main effect of the drop delay levels, suggesting that the decrease in evidence was mainly related to time, and not the experimental manipulation per se.

Importantly, the conjunction analysis indicated that the BOLD activity correlating with decision urgency peaked in the right striatum (Fig. 7a). While the individual drop delay conditions also showed other regions that were activated (Table 5), the striatum was the only region that survived thresholding in the conjunction of the two conditions. It should be noted that the cluster that survived thresholding also extends into anterior insula. However, the peak coordinate of activation clearly lies in striatum (MNI: $x = 32, y = 12, z = 4$).

The individual participant regression coefficients of evidence against decision time were negatively correlated with the BOLD response in striatum, across conditions (Fig. 7b). This effect was not dependent on the undue influence from individual data points, as the 95% confidence interval around the bootstrapped distribution of regression coefficients was completely below zero (Fig. 8). Thus, a more negative slope coefficient in the regression of evidence against decision time reflects a larger BOLD response in striatum. This means that participants with greater striatal activation demonstrated a greater sense of urgency in their decisions. Because this finding is shared across the two drop-delay conditions, the relationship between sense of urgency in behavior and BOLD response in striatum is independent of the duration of the task. This result is consistent with the hypothesis that the striatum is involved in implementing a decision urgency signal.

Table 4
Beta estimates for the linear mixed-effects model of Experiment 2.

Factor	Estimate	Degrees of freedom	t	p
Intercept	0.92	220	66.09	<0.001
Time step	−0.011	35,620	−22.91	<0.001
Time step × 400 ms	−0.0023	35,460	−5.66	<0.001

Discussion

A recent class of dynamic models of decision making in the computational neuroscience literature suggest that decision-makers regulate response selection as a function of time (Bowman et al., 2012; Cisek et al., 2009; Ditterich, 2006a, 2006b; Drugowitsch et al., 2012; Ratcliff and Frank, 2012; Thura et al., 2012). This class of models assumes a decreasing decision threshold, where the quantity of evidence required to trigger a decision decreases with time. This assumption reflects the idea that decision-makers might become less patient, or feel an increasing sense of urgency, as time passes, and will commit to a course of action on the basis of less evidence.

In Experiment 1, we established behavioral evidence that supports the concept of decision urgency. To study urgency, we developed a Bayesian model (the Rate Difference model) that tracks changes in stimulus information over time to compute the quantity of evidence present at the time of decision. We found that the amount of evidence required to trigger a decision decreased with each additional unit of time, leading to choices that were based on less evidence. This behavioral pattern provides support for a decreasing decision threshold, indicating that less evidence is required as time progresses, or as an urgency signal, indicating that a choice should be made independent of whether a decision bound has been reached. Our findings are consistent with previous research in which the amount of information required for a decision was found to decrease with time (Cisek et al., 2009; Gluth et al., 2012; Thura et al., 2014).

The concept of evidence can be quantified in many ways that differ in minor details (Brown et al., 2009; Kira et al., 2015; McMillen and Holmes, 2006; Van Maanen et al., 2012a, 2012b), so it is important to validate the results of the model developed in Experiment 1 in an independent data set. This research strategy strengthens the generalizability of the results, as there is less

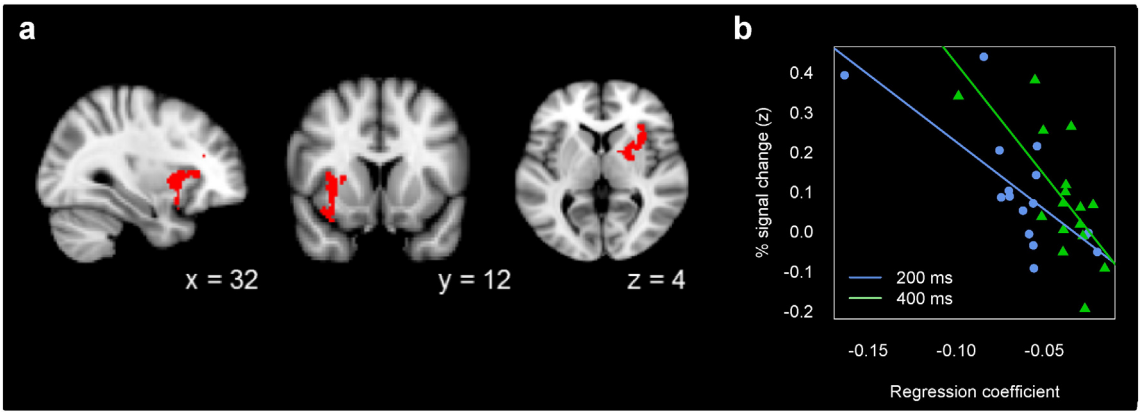

Fig. 7. The striatum reflects decision urgency. (a) A conjunction analysis of both conditions reveals that only activation in the striatum is negatively correlated with regression slopes. Red pixels indicate positive *z* values. Peak coordinates are given in MNI-space. (b) Both conditions show a reliable correlation between *z*-scored percentage signal change in the striatum and the individual regression slopes of evidence against time for both drop delay conditions.

freedom for researcher bias. Experiment 2 replicated the behavioral patterns observed in Experiment 1 and found similar outcomes of the model analysis in that less evidence was required as time progressed within a trial.

In addition to replicating the behavioral findings, we found evidence in Experiment 2 that is consistent with a role for a cortico-basal ganglia network in within-trial decision urgency. In particular, we found that – independently of decision duration – activation in the striatum negatively correlated with the evidence available to participants at the time they committed to a decision. That is, greater striatal activity is associated with greater urgency in behavior. The cortico-basal ganglia network model assumes that the execution of actions is mediated through the basal ganglia nuclei (Mink, 1996). When there is no preference for a course of action, the output nuclei of the basal ganglia inhibit the thalamus and brainstem, precluding the execution of actions (Chevalier et al., 1985; Deniau and Chevalier, 1985). When cortical signals activate the input nuclei of the basal ganglia, most prominently the striatum, the inhibition of the output nuclei are selectively released, allowing specific actions to take place, such as responding in a decision making task. It is therefore conceivable that the striatum acts as a gate (Cools et al., 2006; Frank et al., 2001) that signals a higher degree of urgency. Various mechanisms are proposed by which the mediation of a striatal signal results in action selection (e.g., Cools et al., 2006; Frank et al., 2001; Lo and Wang, 2006). However, our results do not disambiguate between these theoretical proposals.

These results are consistent with the literature on the neural mechanism of the speed-accuracy tradeoff in perceptual decision making, which has shown increased striatal activation when participants are explicitly instructed to emphasize decision speed over accuracy across different trials (Forstmann et al., 2008; Ivanoff et al., 2008; Van Maanen et al., 2011; Van Veen et al., 2008; Winkel et al., 2012). More generally, it seems that individual differences in action selection are reflected by activation of the striatum (e.g., Balleine et al., 2007; Delgado, 2007). For this reason, striatal activity had already been hypothesized to reflect decision urgency in monkeys performing expanded judgment tasks similar to the ones presented in the current study (Thura and Cisek, 2016; Thura et al., 2014). Our findings extend this work by providing clear evidence for the role of striatal activation in the absence of explicit instructions to emphasize one mode of responding over another: when decision-makers were free to establish the cost of the time taken to accumulate evidence to inform their choices.

Previous research has shown that in addition to the striatum, the pre-supplementary motor area (pre-SMA) is involved in setting response thresholds in the speed-accuracy tradeoff (Forstmann et al., 2008; Ivanoff et al., 2008; Van Maanen et al., 2011; Van Veen et al., 2008). Here, we found some evidence for the involvement of the pre-SMA in urgency as well. However, the signal was not as strong as in the striatum, and more dispersed. As a result, it did not appear above threshold in the analyses that we performed. Previous work on time-variant evidence accumulation in the context of economic choices, however, also reported activation in the pre-SMA, in concert with the striatum and insula (Gluth et al., 2012). Therefore, it seems likely that a dynamic adjustment of response thresholds activates the same neural network involved in static manipulations of response thresholds. However, our results suggest that the function of the striatum is more prominent than the function of pre-SMA in dynamic conditions, and that striatum reflects the neural activation of the urgency signal in humans.

Table 5
Significant correlations with individual regression coefficients of evidence versus time, split per drop delay condition.

Condition	Regression	ROI	Voxels	*z*-Value	*x*	*y*	*z*
200 ms	Positive	R Thalamus	844	3.51	8	−22	20
	Negative	R Striatum	1132	4.07	22	4	6
		L Striatum	638	3.45	−30	0	4
		L Inferior frontal cortex	431	3.53	−54	32	−12
400 ms	Positive	L Parahippocampal gyrus	571	3.7	−32	−40	−8
	Negative	R Anterior cingulate cortex	991	4.11	4	22	36
		R Striatum	689	4.03	32	12	2

Note: 200 ms and 400 ms: drop delay condition; *x*, *y*, *z*: peak MNI-coordinates of each reported cluster.

Conflict of interest

The authors declare no competing financial interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2016.06.045.

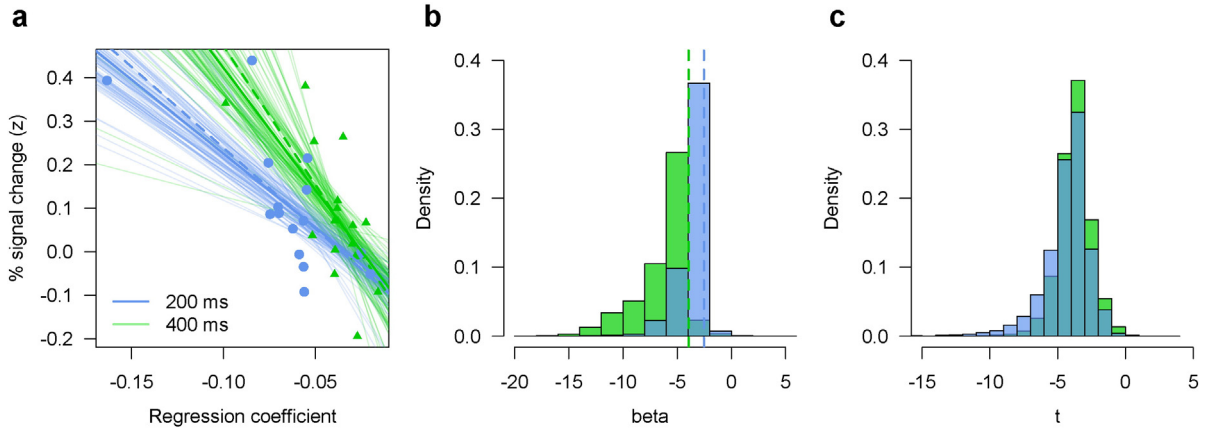

Fig. 8. Robust regression of the evidence coefficient and striatal BOLD. (a) The data (symbols), the default regression (solid lines), the averaged bootstrapped regression (dashed lines), and 100 samples illustrating the distribution of the regression lines. (b) The distribution of regression coefficients. The dashed vertical line represents the 95%-CI upper limit, indicating that these distributions differ from zero. (c) The distribution of *t*-statistics for the regression coefficients. Blue: 200 ms condition; Green: 400 ms condition.

References

Akaike, H., 1974. A new look at the statistical model identification. IEEE Trans. Autom. Control 19, 716–723.

Baayen, R.H., Davidson, D.J., Bates, D.M., 2008. Mixed-effects modeling with crossed random effects for subjects and items. J. Mem. Lang. 59, 390–412.

Balleine, B.W., Delgado, M.R., Hikosaka, O., 2007. The role of the dorsal striatum in reward and decision-making. J. Neurosci. 27, 8161–8165. http://dx.doi.org/10.1523/JNEUROSCI.1554-07.2007.

Bates, D.M., 2005. Fitting Linear Mixed Models in R. R News. p. 5.

Bowman, N.E., Kording, K.P., Gottfried, J.A., 2012. Temporal integration of olfactory perceptual evidence in human orbitofrontal cortex. Neuron 75, 916–927. http://dx.doi.org/10.1016/j.neuron.2012.06.035.

Brown, S.D., Heathcote, A., 2008. The simplest complete model of choice response time: linear ballistic accumulation. Cogn. Psychol. 57, 153–178.

Brown, S.D., Steyvers, M., Wagenmakers, E.-J., 2009. Observing evidence accumulation during multi-alternative decisions. J. Math. Psychol. 53, 453–462.

Busemeyer, J.R., Rapoport, A.M., 1988. Psychological models of deferred decision making. J. Math. Psychol. 32, 91–134.

Chevalier, G., Vacher, S., Deniau, J.M., Desban, M., 1985. Disinhibition as a basic process in the expression of striatal functions. I. The striato-nigral influence on tecto-spinal/tecto-diencephalic neurons. Brain Res. 334, 215–226.

Choi, J.E.S., Vaswani, P.A., Shadmehr, R., 2014. Vigor of movements and the cost of time in decision making. J. Neurosci. 34, 1212–1223. http://dx.doi.org/10.1523/JNEUROSCI.2798-13.2014.

Churchland, A.K., Kiani, R., Shadlen, M.N., 2008. Decision-making with multiple alternatives. Nat. Neurosci. 11, 693–702. http://dx.doi.org/10.1038/nn.2123.

Cisek, P., Puskas, G.A., El-Murr, S., 2009. Decisions in changing conditions: the urgency-gating model. J. Neurosci. 29, 11560–11571. http://dx.doi.org/10.1523/JNEUROSCI.1844-09.2009.

Cools, R., Ivry, R.B., D'Esposito, M., 2006. The human striatum is necessary for responding to changes in stimulus relevance. J. Cogn. Neurosci. 18, 1973–1983. http://dx.doi.org/10.1162/jocn.2006.18.12.1973.

Delgado, M.R., 2007. Reward-related responses in the human striatum. Ann. N. Y. Acad. Sci. 1104, 70–88. http://dx.doi.org/10.1196/annals.1390.002.

Deneve, S., 2012. Making decisions with unknown sensory reliability. Front. Neurosci. 6, 1–13. http://dx.doi.org/10.3389/fnins.2012.00075.

Deniau, J.M., Chevalier, G., 1985. Disinhibition as a basic process in the expression of striatal functions. II. The striato-nigral influence on thalamocortical cells of the ventromedial thalamic nucleus. Brain Res. 334, 227–233.

Ditterich, J., 2006a. Stochastic models of decisions about motion direction: behavior and physiology. Neural Netw. 19, 981–1012. http://dx.doi.org/10.1016/j.neunet.2006.05.042.

Ditterich, J., 2006b. Evidence for time-variant decision making. Eur. J. Neurosci. 24, 3628–3641. http://dx.doi.org/10.1111/j.1460-9568.2006.05221.x.

Drugowitsch, J., Moreno-Bote, R., Churchland, A.K., Shadlen, M.N., Pouget, A., 2012. The cost of accumulating evidence in perceptual decision making. J. Neurosci. 32, 3612–3628. http://dx.doi.org/10.1523/JNEUROSCI.4010-11.2012.

Forstmann, B.U., Dutilh, G., Brown, S.D., Neumann, J., von Cramon, D.Y., Ridderinkhof, K.R., Wagenmakers, E.-J., 2008. Striatum and pre-SMA facilitate decision-making under time pressure. Proc. Natl. Acad. Sci. U. S. A. 105, 17538–17542.

Forstmann, B.U., Ratcliff, R., Wagenmakers, E.-J., 2016. Sequential sampling models in cognitive neuroscience: advantages, applications, and extensions. Annu. Rev. Psychol. 67.

Frank, M.J., Loughry, B., O'Reilly, R.C., 2001. Interactions between frontal cortex and basal ganglia in working memory: a computational model. Cogn. Affect. Behav. Neurosci. 1, 137–160. http://dx.doi.org/10.3758/CABN.1.2.137.

Frazier, P.I., Yu, A.J., 2008. Sequential hypothesis testing under stochastic deadlines. Adv. Neural Inf. Proces. Syst. 20, 465–472.

Gluth, S., Rieskamp, J., Büchel, C., 2012. Deciding when to decide: time-variant sequential sampling models explain the emergence of value-based decisions in the human brain. J. Neurosci. 32, 10686–10698. http://dx.doi.org/10.1523/JNEUROSCI.0727-12.2012.

Gold, J.I., Shadlen, M.N., 2007. The neural basis of decision making. Annu. Rev. Neurosci. 30, 535–574. http://dx.doi.org/10.1146/annurev.neuro.29.051605.113038.

Grinband, J., Wager, T.D., Lindquist, M., Ferrera, V.P., Hirsch, J., 2008. Detection of time-varying signals in event-related fMRI designs. NeuroImage 43, 509–520. http://dx.doi.org/10.1016/j.neuroimage.2008.07.065.

Haith, A.M., Reppert, T.R., Shadmehr, R., 2012. Evidence for hyperbolic temporal discounting of reward in control of movements. J. Neurosci. 32, 11727–11736. http://dx.doi.org/10.1523/JNEUROSCI.0424-12.2012.

Hanks, T.D., Kiani, R., Shadlen, M.N., 2014. A neural mechanism of speed-accuracy tradeoff in macaque area LIP. Elife 2014, e02260. http://dx.doi.org/10.7554/eLife.02260.

Hawkins, G.E., Brown, S.D., Steyvers, M., Wagenmakers, E.-J., 2012a. Decision speed induces context effects in choice. Exp. Psychol. 59, 206–215.

Hawkins, G.E., Brown, S.D., Steyvers, M., Wagenmakers, E.-J., 2012b. Context effects in multi-alternative decision making: empirical data and a Bayesian model. Cogn. Sci. 36, 498–516. http://dx.doi.org/10.1111/j.1551-6709.2011.01221.x.

Hawkins, G.E., Brown, S.D., Steyvers, M., Wagenmakers, E.-J., 2012c. An optimal adjustment procedure to minimize experiment time in decisions with multiple alternatives. Psychon. Bull. Rev. 19, 339–348. http://dx.doi.org/10.3758/s13423-012-0216-z.

Hawkins, G.E., Forstmann, B.U., Wagenmakers, E.-J., Ratcliff, R., Brown, S.D., 2015. Revisiting the evidence for collapsing boundaries and urgency signals in perceptual decision-making. J. Neurosci. 35, 2476–2484.

Irwin, F., Smith, W.A., Mayfield, J.F., 1956. Tests of two theories of decision in an expanded judgment situation. J. Exp. Psychol. 51, 261–268.

Ivanoff, J., Branning, P., Marois, R., 2008. fMRI evidence for a dual process account of the speed-accuracy tradeoff in decision-making. PLoS One 3, e2635. http://dx.doi.org/10.1371/journal.pone.0002635.

Jeffreys, H., 1961. The Theory of Probability. Oxford UP.

Jenkinson, M., Bannister, P., Brady, M., Smith, S., 2002. Improved optimization for the robust and accurate linear registration and motion correction of brain images. NeuroImage 17, 825–841.

Kira, S., Yang, T., Shadlen, M.N., 2015. A neural implementation of Wald's sequential probability ratio test. Neuron 85, 861–873.

Koch, I., Ruge, H., Brass, M., Rubin, O., Meiran, N., Prinz, W., 2003. Equivalence of cognitive processes in brain imaging and behavioral studies: evidence from task switching. NeuroImage 20, 572–577.

Lo, C.C., Wang, X.J., 2006. Cortico-basal ganglia circuit mechanism for a decision threshold in reaction time tasks. Nat. Neurosci. 9.

McMillen, T., Holmes, P., 2006. The dynamics of choice among multiple alternatives. J. Math. Psychol. 50, 30–57.

Mink, J.W., 1996. The basal ganglia: focused selection and inhibition of competing motor programs. Prog. Neurobiol. 50, 381–425.

Mulder, M.J., Van Maanen, L., Forstmann, B.U., 2014. Perceptual decision neurosciences - a model-based review. Neuroscience 277, 872–884.

Nichols, T., Brett, M., Andersson, J., Wager, T.D., Poline, J.-B., 2005. Valid conjunction inference with the minimum statistic. NeuroImage 25, 653–660. http://dx.doi.org/10.1016/j.neuroimage.2004.12.005.

Ratcliff, R., 1978. A theory of memory retrieval. Psychol. Rev. 85, 59–108.

Ratcliff, R., Frank, M.J., 2012. Reinforcement-based decision making in corticostriatal circuits: mutual constraints by neurocomputational and diffusion models. Neural Comput. 24, 1186–1229. http://dx.doi.org/10.1162/NECO_a_00270.

Rouder, J.N., Morey, R.D., Speckman, P.L., Province, J.M., 2012. Default Bayes factors for ANOVA designs. J. Math. Psychol. 56, 356–374.

Schwarz, G., 1978. Estimating the dimension of a model. Ann. Stat. 6, 461–464.

Thura, D., Cisek, P., 2016. Modulation of premotor and primary motor cortical activity during volitional adjustments of speed-accuracy trade-off. J. Neurosci. 36, 938–956.

Thura, D., Beauregard-Racine, J., Fradet, C.-W., Cisek, P., 2012. Decision making by urgency gating: theory and experimental support. J. Neurophysiol. 108, 2912–2930. http://dx.doi.org/10.1152/jn.01071.2011.

Thura, D., Cos, I., Trung, J., Cisek, P., 2014. Context-dependent urgency influences speed-accuracy trade-offs in decision-making and movement execution. J. Neurosci. 34, 16442–16454. http://dx.doi.org/10.1523/JNEUROSCI.0162-14.2014.

Turner, R.S., Desmurget, M., 2010. Basal ganglia contributions to motor control: a vigorous tutor. Curr. Opin. Neurobiol. 20, 704–716. http://dx.doi.org/10.1016/j.conb.2010.08.022.

Usher, M., McClelland, J.L., 2001. The time course of perceptual choice: the leaky, competing accumulator model. Psychol. Rev. 108, 550–592.

Van Maanen, L., Brown, S.D., Eichele, T., Wagenmakers, E.-J., Ho, T.C., Serences, J.T., Forstmann, B.U., 2011. Neural correlates of trial-to-trial fluctuations in response caution. J. Neurosci. 31, 17488–17495.

Van Maanen, L., Grasman, R.P.P.P., Forstmann, B.U., Keuken, M.C., Brown, S.D., Wagenmakers, E.-J., 2012a. Similarity and number of alternatives in the random-dot motion paradigm. Atten. Percept. Psychophys. 74, 739–753.

Van Maanen, L., Grasman, R.P.P.P., Forstmann, B.U., Wagenmakers, E.-J., 2012b. Piéron's law and optimal behavior in perceptual decision-making. Front. Decis. Neurosci. 5 (Article 143).

Van Maanen, L., Forstmann, B.U., Keuken, M.C., Wagenmakers, E.-J., Heathcote, A., 2016. The impact of MRI scanner environment on perceptual decision making. Behav. Res. Methods 48, 184–200.

Van Veen, V., Krug, M.K., Carter, C.S., 2008. The neural and computational basis of controlled speed-accuracy tradeoff during task performance. J. Cogn. Neurosci. 20, 1952–1965. http://dx.doi.org/10.1162/jocn.2008.20146.

Vickers, D., 1979. Decision Processes in Visual Perception. Academic Press, London.

Winkel, J., Van Maanen, L., Ratcliff, R., der Schaaf, M.E., Van Schouwenburg, M.R., Cools, R., Forstmann, B.U., 2012. Bromocriptine does not alter speed-accuracy tradeoff. Front. Decis. Neurosci. 6 (Article 126).

Zhang, S., Lee, M.D., Vandekerckhove, J., Maris, G., Wagenmakers, E.-J., 2015. Time-varying boundaries for diffusion models of decision making and response time. Front. Psychol. 5, 1364.