Report

Noise and Correlations in Parallel Perceptual Decision Making

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Summary

Perceptual decisions involve the accumulation of sensory evidence over time, a process that is corrupted by noise [1]. Here, we extend the decision-making framework to crossmodal research [2, 3] and the parallel processing of two distinct signals presented to different sensory modalities like vision and audition. Contrary to the widespread view that multisensory signals are integrated prior to a single decision [4-10], we show that evidence is accumulated for each signal separately and that consequent decisions are flexibly coupled by logical operations. We find that the strong correlation of response latencies from trial to trial is critical to explain the short latencies of multisensory decisions. Most critically, we show that increased noise in multisensory decisions is needed to explain the mean and the variability of response latencies. Precise knowledge of these key factors is fundamental for the study and understanding of parallel decision processes with multisensory signals.

Results

Research on perceptual decision making has converged on a general framework that provides an excellent account for the exact timing of decision-making behavior [1]. The basic principle is that noisy evidence for a sensory signal is accumulated over time until a criterion is reached and a decision is made [11–19]. The framework is particularly successful because evidence accumulation (or sequential sampling) not only is optimal in that it is the fastest decision maker for a given level of accuracy [15, 20] but also provides a straightforward explanation for many robust empirical findings like the right-skewed nature of latency distributions [12, 13] and speed-accuracy trade-offs [14, 19]. Moreover, it is biologically plausible because some neurons increase their firing rates over time similarly to the accumulation of evidence in decision-making models [21–23].

One of the key aspects of the framework is noise [24, 25]. The presence of noise is evident because response latencies, even with highly salient signals, are extremely variable [26]. We show here that a careful analysis of noise is especially critical when decisions rely on more than one signal at a time. We consider here a task adapted from crossmodal research [4, 27] that requires participants to detect the common onset of motion and sound signals that are embedded in a continuous audiovisual background (Figure 1A). This so-called redundant condition (R_{MS}) is randomly interleaved with two

single conditions, in which only the sound (Ss) or only the motion signal (S_M) is presented (Figure 1B). By design, the two signals are coupled by a logical OR operator. In other words, signals are "redundant" in the sense that detection of either signal is sufficient for a correct response. According to models of perceptual decision making like the simple linear approach to threshold with ergodic rate (LATER) model [12, 13], evidence for single signals is accumulated until a criterion is reached and a response is triggered (Figures 1C and 1D). The accumulation process is corrupted by Gaussian noise so that response latencies on a given trial are unpredictable but overall follow a recinormal distribution [13]. On presentation of a redundant signal, race models predict that a response is triggered by the faster of two parallel decision processes [28]. Consequently, the overall latency distribution should follow the minimum function of the distributions in single conditions (Figure 1E). Interestingly, this straightforward prediction based on probability summation provides a direct link between single and redundant conditions that can be used to compare decision processes when signals and decision criteria—the factors that are typically manipulated in studies on decision making—are not changed. The critical difference is that evidence is accumulated only for one signal in single but simultaneously for two in redundant conditions. By focusing on the difference between empirical and predicted distributions, it is then possible to investigate how simultaneous decision processes interact to guide coherent actions and, particularly, whether noise has changed.

The Redundant Signal Effect

Fifteen human participants indicated the onset of any sound or motion signal via manual key presses. The task was easy and performance close to perfect (averaged across conditions; hits: >99%, false alarms: ~2%). In 60 blocks, we collected latencies of 50 valid responses for each condition (four blocks per participant; 3,000 responses per condition). Responses in condition R_{MS} are on average faster compared to conditions S_M and S_S (Figure 2A). This speed-up, called the redundant signal effect, is traditionally analyzed using cumulative distribution functions. The use of cumulative probabilities is convenient because it allows us to check Miller's test [4]. Following Boole's inequality, distributions in redundant conditions cannot exceed the sum of distributions in corresponding single conditions, with the assumption that there were no interactions between the signals [26, 29]. To obtain reliable distribution functions, we rank ordered the latencies of each block and averaged rank/quantile latencies across blocks (Vincent averaging [30]; see Supplemental Experimental Procedures available online). To obtain continuous distribution functions, we fitted recinormal distributions to the group quantiles (a list of distributions can be found as Table S1). Consistent with the numerous follow-up studies of [4], we found that fastest latencies in condition R_{MS} exceeded the sum of distributions in conditions S_M and S_S, suggesting that an interaction has occurred (Figure 2B; for analogous results with color and sound signals, see Figure S2). Interestingly, violations of Boole's inequality have contributed to the deeply entrenched and widespread view that the simultaneous

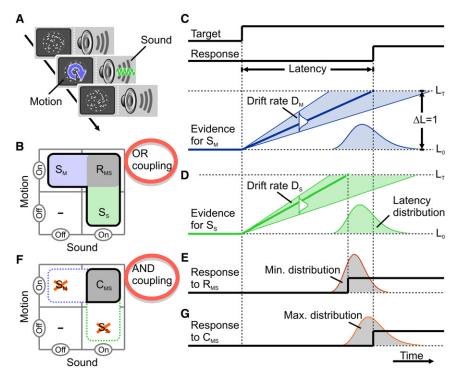


Figure 1. Paradigm and Model

(A) Participants indicated the onset of target signals (motion or sound; see B) embedded in a continuous audiovisual background. Except for stimulus onset, these distinct signals did not refer to a common environmental property.

(B) In two single conditions, either the motion (S_M) or the sound (S_S) was presented. In a redundant condition, both signals were presented at the same time $(R_{MS};$ see A). The two signals were coupled by a logical OR operator, and detection of either signal was sufficient for a correct response.

(C) On presentation of S_{Mr} , evidence for motion is accumulated from the start level L_0 until the threshold L_T is reached and a response is triggered. The drift rate is subject to Gaussian noise. The resulting latency distribution follows the reciprocal of the Gaussian, which is a recinormal distribution that is skewed to the right like empirical distributions.

(D) Evidence for the sound signal is accumulated analogously.

(E) On presentation of R_{MS} , a speed-up of latencies is expected because a response can be triggered by the faster of the two parallel decision processes (in the illustrated trial, when evidence for sound reaches L_T). The resulting latency distribution is predicted by the minimum function of the distributions in (C) and (D). Model predictions for cumulative latency distributions are shown as Figure S1.

(F) In an additional condition, targets were defined by a conjunction of motion and sound (C_{MS}). Participants had to withhold a response on presentation of single signals. Hence, the two signals were coupled by a logical AND operator.

(G) On presentation of C_{MS} , a slowdown of latencies is expected because a response can be triggered only after both signals have been detected (in the illustrated trial, when evidence for motion reaches L_T). The resulting latency distribution is predicted by the maximum function of the distributions in (C) and (D).

processing of distinct multisensory signals is even faster than would be predicted from the individual signals [3], which supposedly requires that signals are integrated, i.e., that evidence for distinct signals is pooled within a single decision process [4]. In stark contrast, we provide an alternative interpretation according to which distinct signals are not integrated but mutually interact by increased noise, yielding not faster but more variable responses.

Correlations and Trial History

To identity possible interactions, we aimed for an exact prediction of the latency distribution in condition R_{MS} using probability summation. Let $P(T\!\leq\!t|S_M)$ and $P(T\!\leq\!t|S_S)$ be the cumulative probabilities that a response with latency ${\it T}$ less than time ${\it t}$ has been triggered in conditions S_M and S_S , respectively. Then, in condition R_{MS} , the probability $P(T\!\leq\!t|R_{MS})$ that a response to one or the other signal has been triggered can be computed from

$$P(T \leq t|R_{MS}) = P(T \leq t|S_M) + P(T \leq t|S_S) - P(T \leq t|S_M \cap T \leq t|S_S). \tag{Equation 1}$$

The joint probability $P(T \le t | S_M \cap T \le t | S_S)$ is given by the product of $P(T \le t | S_M)$ and $P(T \le t | S_S)$ if response latencies to single signals are statistically independent, an assumption rarely explicitly checked.

To address the issue of independence, we examined trial-to-trial dependencies. Consistent with research on task switching [31–33], we found that latencies depended on the signal presented on the previous trial (Figure 3A). In condition S_M, latencies were shorter when following a motion compared to

a sound signal. The opposite effect occurred in condition $S_{\rm S}$. To show how the history effect is reflected in the latency distribution, we performed a correlation analysis on the basis of the group quantiles that represent the cumulative distributions (see Figure 2B). For the 60 responses that were summarized by a quantile, we counted responses that were preceded by conditions $S_{\rm M}$, $S_{\rm S}$, and $R_{\rm MS}$, respectively. Based on these counts, we computed the relative frequency of motion signals

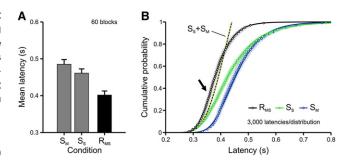


Figure 2. The Redundant Signal Effect

(A) Mean latencies to R_{MS} were faster compared to S_M and S_S (mean and SEM of 60 blocks with 50 latencies each).

(B) Cumulative distributions are presented with circles and shaded areas indicating group quantiles with SEM and best-fitting recinormal distributions shown as solid lines. The shift of the $R_{\rm MS}$ distribution to the left corresponds to the speed-up of mean latencies (see A). Numerous $R_{\rm MS}$ quantiles exceeded the theoretical bound provided by the sum of the distributions in conditions $S_{\rm M}$ and $S_{\rm S}$ (arrow). Analogous results with color and sound signals are shown in Figure S2.

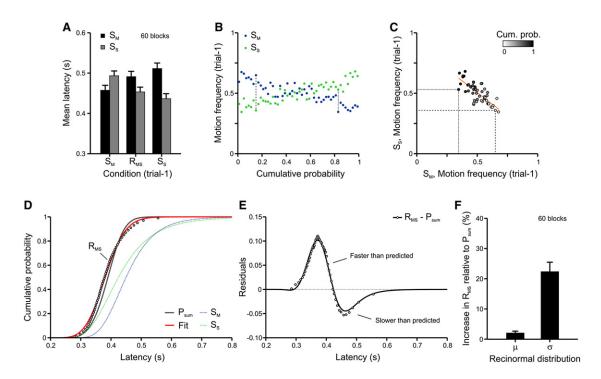


Figure 3. Interactions

- (A) Mean latencies (with SEM) in conditions S_M and S_S as a function of the condition that was presented on the previous trial.
- (B) For each group quantile of the cumulative probabilities shown in Figure 2B, we computed the relative frequency that motion (rather than sound) signals were presented previously. This "motion frequency" is close to one (zero) if mostly motion (sound) signals were presented.
- (C) Plotting motion frequencies for each quantile in condition S_M against S_S (as exemplified by the broken lines; see B) reveals a negative correlation between latencies in single conditions when signals are randomly switched. Cum. prob., cumulative probability.
- (D) Based on conditions S_M and S_S , we fitted the model with the correlation coefficient ρ as a free parameter to the distribution in condition R_{MS} . The empirical distribution deviated from the best-fitting model (P_{sum}), in that most quantiles were faster except for the slowest quantiles that were slower than predicted. Hence, the empirical distribution was overall more variable than predicted (see also E and F). We extended the model to allow for additional noise η when two signals are processed simultaneously. The extended model fitted the empirical distribution reasonably well (Fit).
- (E) The deviation of empirical latencies from P_{sum} is best illustrated by the difference between the two distributions.
- (F) We tested the deviation based on the parameters of recinormal distributions fitted to the empirical and predicted quantiles of each block. Whereas the mean μ was slightly elevated (i.e., responses were on average faster than predicted), the standard deviation σ was greatly increased (i.e., latencies were much more variable than predicted). Error bars indicate SEM.

Analogous results with color and sound signals are shown in Figure S3.

on the previous trial. Inspection of motion frequencies across quantiles revealed that fast quantiles in single conditions included mostly responses when signals were repeated (Figure 3B). In contrast, the slow quantiles included mostly responses when signals were switched. The resulting correlation is best illustrated by plotting the motion frequency in condition S_M against condition S_S for each quantile (Figure 3C). This analysis showed that trial history manifests a strong negative correlation between latencies in single conditions (Pearson's linear correlation coefficient, $\rho_H = -0.76$, p < 0.0001; for analogous results with color and sound signals, see Figure S3; history effects can last even longer than trial-1; data not shown). Within the accumulation framework, such history effects may arise when for example threshold levels and/or drift rates systematically vary in an antipodal manner. Critically, this analysis shows that predictions based on probability summation have to consider potential correlations.

Within the framework illustrated in Figure 1, predictions based on probability summation are given by the minimum function of latency distributions in single conditions or, equivalently, by the maximum function of the corresponding drift rate distributions. The use of drift rates is convenient here because predictions can be computed from the exact maximum function of two Gaussian random variables, taking into

account a correlation coefficient ρ [34]. We fitted this model constrained by the single-signal distributions and with ρ as a free parameter to the empirical distribution in condition R_{MS} (Figure S1 shows simulations in which ρ is systematically varied). As expected from the trial history analysis, the latency distribution was best explained assuming a negative correlation (ρ = -0.70; see Figure 3D; for best-fitting parameters, see Table S2).

Noise

Although the best fit was already close to the empirical distribution, the two deviated from each other in that fastest responses were faster and slowest slower than predicted, which is best visualized by the difference between the two distributions (Figure 3E). We analyzed this deviation based on the 60 individual blocks of trials. For each block, we fitted recinormal distributions to both the empirical and the predicted distribution. We found that the empirical mean (μ) was slightly larger than predicted (Figure 3F; one-sample t test, p = 0.0002). This small but robust difference translated into an additional speed-up of the empirical median latency of about 8 ms. More prominently, the empirical standard deviation (σ) was much larger than predicted (Figure 3F; one-sample t test, p < 0.0001). In summary, latencies differed from

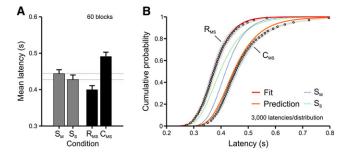


Figure 4. Predictions

We presented conditions in separate blocks (S_M , S_s , and R_{MS} ; see Figures 1A and 1B). We included also a new condition in which targets were defined by a signal conjunction (C_{MS} , see Figure 1F).

(A) Mean latencies. Whereas responses in condition R_{MS} were sped up, responses in condition C_{MS} were slowed down. Mean and SEM of 60 blocks are shown.

(B) Cumulative distributions. The extended model provided an excellent fit for condition R_{MS} . A straightforward prediction to condition C_{MS} is that latencies should follow the maximum function of the distributions in single conditions (Figure 1G). Strikingly, the empirical distribution was very close to the prediction using the correlation and noise parameters as fitted in condition R_{MS} .

Analogous results with color and sound signals are shown in Figure S4.

probability summation in two ways: they were slightly faster and, most notably, much more variable than predicted (for analogous results with color and sound signals, see Figure S3).

How can increased variability be explained? For predictions, we have so far assumed that the variability as determined in single conditions is not changed in redundant conditions. This assumption seemed reasonable given that physical signals were identical. Moreover, because conditions were randomly interleaved, participants could not anticipate signals, and it is probably safe to assume that both the starting level and the decision threshold were constant across conditions (see S_0 and S_1 in Figures 1C and 1D). However, it is plausible that the internal noise has changed in redundant conditions. To illustrate such an effect, we extended the model by allowing the internal noise to increase (which we simulate by the interaction noise η that is added in the redundant condition to the standard deviations of the drift rates D_M and D_S as determined in single conditions). Interestingly, with increasing noise the model predicts both a slight speed-up and an increased variability of response latencies including violations of Boole's inequality (Figure S1).

To demonstrate that probability summation and increased noise can explain the redundant signal effect, we fitted our model to the empirical distribution in condition R_{MS}. The model was constrained by the latency distributions in the single conditions and had just two degrees of freedom: the correlation coefficient ρ and the interaction noise η . The model fitted the empirical distribution reasonably well (Figure 3D; for analogous results with color and sound signals, see Figure S3). Regarding the correlation, the best-fitting estimate ($\rho = -0.59$) differed only slightly from the estimate without additional noise $(\rho = -0.70)$; for best-fitting parameters, see Table S2). Interestingly, regarding noise, the best-fitting estimate indicated that the noise level was largely increased when evidence for two signals was accumulated at the same time ($\eta = 0.10 \text{ s}^{-1}$, corresponding to an increase of ~23% compared to the average standard deviation of drift rates in single conditions). In summary, the variability of latencies in redundant conditions was

largely increased compared to probability summation, which may indicate that a significant fraction of the internal noise was the product of the decision processes themselves.

Predictive Power

Our findings allow for straightforward predictions that can easily be tested. First, we argued that the negative correlation is related to trial history. To test this claim, we conducted a second experiment in which conditions were presented in separate blocks. Although responses were again sped up (Figure 4A), we expected the history effect to disappear because signals were not randomly switched. The model fitted to the condition R_{MS} confirmed this prediction (Figure 4B). Critically, while the noise was again increased ($\eta = 0.06 \, \text{s}^{-1}$, corresponding to $\sim 15\%$ of the average standard deviation of drift rates in single conditions), the estimated correlation was slightly positive ($\rho = 0.21$; for analogous results with color and sound signals, see Figure S4). A small positive correlation may relate, for example, to the motor act or other common sources of variability that contributed to the overall variability of latencies.

The block design allowed for another, even more compelling prediction. We argue that evidence is accumulated separately for each signal and that consequent decisions are coupled by a logical OR operator. If evidence is indeed accumulated separately, it should be possible to couple decisions by other logical operations. To test this hypothesis, we included a new condition in which targets were defined by a conjunction of motion and sound signals. Here, participants had to press a key when both signals were presented but to withhold a response on presentation of either signal (Figure 1F, condition C_{MS}). Note that physical signals in conditions C_{MS} and R_{MS} were identical. However, while responses in condition R_{MS} were sped up, responses in condition C_{MS} were slowed down (Figure 4A). The key difference explaining this effect is that signals in condition C_{MS} were coupled by a logical AND instead of a logical OR operator. Consequently, both signals need to be detected for a correct response, and the cumulative probability $P(T \le t | C_{MS})$ corresponds to

$$P(T \le t | C_{MS}) = P(T \le t | S_M \cap T \le t | S_S).$$
 (Equation 2)

Using the minimum instead of the maximum function of drift rates in single conditions (corresponding to the maximum instead of the minimum function of the latency distributions; see Figure 1G), the distribution in condition C_{MS} should be fully predicted using the best-fitting correlation and noise estimates of condition R_{MS} . Strikingly, the empirical distribution followed this parameter-free prediction remarkably well (Figure 4B; for analogous results with color and sound signals, see Figure S4). These findings provide strong evidence for the flexible coupling of separate decisions on distinct multisensory signals.

Discussion

We extended the framework of perceptual decision making to crossmodal research and the parallel processing of distinct signals. Using probability summation as a link, we compared the timing of decision processes in conditions with identical signals and decision criteria. The critical difference is that only one signal is processed in single conditions but two signals are processed simultaneously in redundant and conjunction conditions. To derive exact predictions, we first analyzed latencies to single signals that are known to depend on trial

history [31–33]. We found that trial history manifests a negative correlation that needs to be considered. Based on predictions that allow for correlations, our central finding is that parallel decision processes interact by increased noise.

Our estimates of the additive interaction noise in the tested audiovisual conditions are in the range of 15%–30% compared to single conditions. It is often argued that evidence accumulation has its substrates in neurons that increase firing rates over time on presentation of a single signal [21–23]. With redundant signals, two pools of neurons would be needed to accumulate evidence for distinct signals separately. It is possible that the increasing activity within these pools mutually produces noise, which is not present when evidence is accumulated for one signal only.

Although we can only speculate about noise sources, increased noise may point to a fundamental capacity limit for parallel processing. According to studies on central processing bottlenecks [35, 36], the capacity to perform different tasks on distinct signals is highly limited. In our study, participants performed always the same action (a button press) but still had to process two signals in redundant and conjunction conditions. If the noise level is increasing with the number of signals being processed, then at some point, performance is expected to degrade due to increasing error rates. Although we have focused on salient signals that yielded ceiling performance, such effects should be particularly visible with weaker signals yielding performance at the threshold level.

Regarding our modeling approach using the LATER model [12, 13], we should note, however, that its simplistic nature is not compatible with the variance of neurons involved in decision making [37]. The model also assumes that accumulation starts with stimulus onset, which leads to a response as soon as the threshold is reached, but actual decision times are probably shorter [18]. Importantly for our scope, the LATER model provided very reasonable fits to the empirical latency distributions in single conditions, which is critical for predictions based on probability summation.

Our study has significant implications for crossmodal research [2, 3] that may be extended to the coupling or binding of distinct signals in general [38]. First, a widespread view is that distinct multisensory signals are integrated, i.e., that pooled evidence is accumulated within a single decision process. Major support for this view comes just from the redundant signal paradigm because latencies in redundant conditions systematically violate the theoretical bound given by Boole's inequality (Figure 2B; see the numerous follow-up studies of [4]). Therefore, in contrast to studies on accuracy [39, 40], it is classically argued that processing of multisensory signals is faster than probability summation and that only synergistic effects due to integrative processing can explain the speed-up of latencies. However, by making these claims, one makes the assumption that the internal noise level is constant. In stark contrast, our systematic analysis of response latencies indicates that noise is increased in redundant compared to single conditions, which explains not only the violation of Boole's inequality but also, for the first time, entire latency distributions with redundant signals.

Second, the redundant signal paradigm has attracted strong interest because studies using electroencephalography have shown multisensory interactions as early as 40 ms after stimulus onset [7, 8, 41]. These findings have contributed to the view that fast feedforward integration takes place in brain areas that are traditionally considered to be unisensory [42, 43]. We argue that two key interactions, related

respectively to trial history and increased noise, occur in the processing of distinct multisensory signals and, thus, may be responsible for these effects. For example, early interactions may relate to trial history, which would imply that early multisensory interactions are rather feedback than feedforward because they depend on previously presented signals and the actual state of the observer. Interestingly, a recent electrophysiological study using auditory and tactile signals has shown that the activity of some neurons in early sensory cortices is affected by signals in the nonpreferred modality [44]. This effect is, however, unspecific regarding stimulus features and may thus relate to the proposed noise interaction.

Finally, our findings with redundant signals translate directly to a task that defines targets by a conjunction of signals. Here, a pooling of signals within a single decision process would cause serious problems because both signals need to be detected to solve the task correctly. In contrast, we argue that separate decisions on distinct signals can be flexibly coupled by AND/OR decision gates, which accounts nicely for latencies in redundant and conjunction tasks. We like to highlight that a flexible coupling would also allow for other combination rules including a weighting of signals as proposed in the context of optimal cue combination [45-47]. Whereas research on the redundant signal effect has focused on latencies with distinct signals, research on optimal cue combination has focused on accuracy with signals that refer to a common environmental property. Despite the direct link between speed and accuracy of decisions on single signals [14, 19], it will be challenging to study speed-accuracy tradeoffs in multisensory decisions because these may depend not only on the nature of signals but also on potential changes in combination rules.

Experimental Procedures

Participants

Fifteen human subjects (eight females, seven males) took part in the two experiments. Participants were aged between 21 and 33 years and had self-reported normal hearing and normal or corrected-to-normal vision. All but one participant (T.U.O.) were naive to the purpose of the experiment. All participants gave informed consent prior to the experiment. The study was approved by the Université Paris Descartes Ethics Committee and was conducted in agreement with the Declaration of Helsinki.

Detailed description of experimental procedures, latency analysis, and the modeling approach can be found in Supplemental Experimental Procedures.

Supplemental Information

Supplemental Information includes four figures, two tables, and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2012.05.031.

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