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Introduction

In the past decade, Bayesian models have received growing interest for their ability to account for a number of psychophysical and sensory motor experimental data (Barlow, 2001; Weiss et al, 2002; Mamassian et al, 2002; Ernst & Banks, 2002).

The main idea behind subjective probabilistic reasoning is that the subject, or the agent, has not the required resources and has not access to all necessary variables and parameters to build a complete model of the world. A change in light intensity impinging on a single photoreceptor cell in the retina might result from an indefinite number of physical causes: variation of the primary light sources, multiple reflection, absorption, refraction of light, object and eye movements, etc... Therefore, it’s simpler and more efficient to build an incomplete, but probabilistic model describing the known, assumed or observed statistical relationships between relevant variables. These relevant variables might have little to do with physical variables, but constitute key elements to guide the action. We are expert in detecting the presence of complex objects in the environment (like fruits or human voice), while psychophysical experiments reveal a number of mistakes or illusions when subjects are asked to report elementary characteristics like stimulus color, velocity or frequency.

The subjective knowledge expression, i.e. the set of probabilistic conditional relationships between variables, might also strongly differ from physical links between variables (i.e. from causes to consequences). In Pavlovian conditioning, animals learn to associate an arbitrary sensory cue (a light, a sound) to a reward or a punishment. One can hardly imagine during conditional learning, animals built a complete causal description of the experimental set-up and protocol which has artificially produce the link between cue and reward. Instead, it is sufficient for the animal to observe the statistical regularity of cue and reward occurrences.

As already proposed by Helmholtz, the statistical characteristics of our environment have an obvious influence on the way we perceive it. In some cases, natural statistics result from fondamental physical laws. For instance, animals have been exposed to gravity forces from life origin; they have developed anti-gravity reflex as well as vestibular and visual processsing which are adapted
to this constraint. McIntyre et al (2001) have shown that we use an internal model of gravity acceleration when we have to anticipate the future position of a free falling object. In other cases, however, our perception can be influenced by purely incidental statistical characteristics. Haijang et al (2006), have shown that a kind of Pavlovian conditioning can also change the 3D perception. They trained subjects with unambiguous 3D objects paired with a contingent signal. After training, subjects were tested with ambiguous 3D objects (a rotating Necker’s cube) and they show that some contingent signals were able to bias the perceptive response towards the most correlated 3D percept. This type of perceptual learning differ from previously described phenomenon like adaptation (prolonged exposure to a given stimulus decreases the sensitivity to that stimulus) or practice (improvement of discrimination with training).

If observers can learn contingent statistics, one can wonder how this newly acquired permanent knowledge is stored, and how it is exploited. In the usual Bayesian models of perception (e.g. Kersten & Yuille, 2003), natural statistics about the environment are expressed in the prior distribution. Afterwards, in each occurrence, the prior distribution is combined with the likelihood, i.e. the probability of observing such sensory data giving the percept, to provide the evaluation of a posterior distribution, i.e. the probability of such percept given the set of sensory data. Probabilistic reasoning, however, does not reduce to this well-known Bayes’s rule.

Yet, the other rule of probabilistic reasoning, namely the marginalization rule, can be experimentally tested. Indeed, the marginalization rule is implicitly used in probabilistic models that are built with more variables than the number of reported behavioural or psychological judgements. For instance, in Bayesian filters such as the one used for explaining the vestibular signal processing (Laurens & Droulez, 2007), the state variables at previous times are marginalized. In the model of structure-from-motion perception (Colas et al, 2007), the object motion with respect to the observer is a state variable that has to be marginalized to get the probability distribution over the tilt and slant variables, that are the ones subjects are asked to report in this kind of experiments. The fact that these models can efficiently account for the reported perception is a strong argument in favour of probabilistic reasoning, but it does not constitute a direct evidence for the use of the marginalization rule per se. In this work, we have designed a more direct way to test this hypothesis. More specifically, we have tried to evaluate the effect of contingent cue suppression after perceptual conditioning. Following the idea of Haijang et al (2006), we have trained human subjects to detect the direction of global motion in partially coherent random dot kinematograms (RDK) in presence of a couple of contingent color cues. During training, the motion coherence of RDK was small but sufficient to perceive a clear directional bias towards left or right (Braddick, 1974). The directional bias was statistically paired to colour cue conjunction. For instance, when the screen was blue on top of the RDK window and yellow below, the motion direction was to the right in 80 % of trials. In test trials, the motion coherence was set to zero, so that subjects should normally respond at random in a two-alternative force choice task. Furthermore, in some trials, one or both
colour cues were absent. Subjects responses in test trials with both colour cues were expected to be biased according to the perceptual conditioning rule (i.e. a bias toward “right” when exposed to the blue-yellow conjunction). Moreover, subjects responses in test trials without one or both colour cues can be predicted from the computation of the marginal probability. If subjects responses match this prediction, this means that cue combination statistics are stored in a way that allow a fully operational probabilistic reasoning.

Methods

Subjects

Two groups of 8 subjects participate to the experiment. All subjects gave informed consent. Both groups follow the same experimental procedure, the only difference was the type of equipment used for display and eye movement monitoring.

Apparatus and display

The whole sequence of trials was computer generated and displayed on either a 53 × 30 cm LCD monitor (Dell 2405FPW) for the 1st group or a 35 × 26 cm CRT monitor for the 2nd group. The visual stimulus, including the RDK circular window (diameter 10 cm) and the surrounding colour cues formed a 12 × 12 cm square in both groups. Subjects was seated at about 70 cm from the screen, and the eye level was adjusted to the center of the screen, so that the visual stimulus covered a visual angle of 10 deg in both horizontal and vertical direction. In the 2nd group, eye movements were monitored with an Eye-Link II oculometer. Trials were rejected when a saccade occured during the RDK display.
Stimuli, task and experimental procedure

All subjects performed a unique session of 320 trials including first 100 learning trials, then 220 test trials. Each trial consists in a sequence of 4 displays (Fig.1): (i) a dark screen with a random duration between 1.5 and 3 sec. (ii) a fixation cross at the centre dark circular window, surrounded by either 2, 1 or 0 colour cues (blue or yellow) during 1 sec. (iii) the fixation cross is removed and the RDK is displayed (together with the colour cues) during 0.4 sec. (iv) a black screen with a quoted mark to inform the subject that he/she has to push the “right” or “left” key on the computer keyboard. A maximal delay of 3 sec. is allowed to for subject’s response.

RDK was composed of 20000 dots, though only about 1500 were visible within the circular window. The motion direction were uniformly drawn except for a given percentage of dots (equal to the coherence ratio) for which the direction was either to the right or to the left. All dots have the same apparent velocity (1.7 deg/sec). The coherence ratio was fixed to 50 % for the first 10 learning trials, then to 30 % for the remaining 90 learning trials, and finally set to 0 % for the test trials. During the test phase, some of the trials (from 10 to 30) were shown and analyzed as learning trials, i.e. the coherence ratio was reset to 30 %. Subjects were not informed of the coherence ratio change.

During the learning phase, a predefined statistical bias was associated with each of the four colour cue combinations. For three among the four cue combinations (e.g. blue/blue, blue/yellow and yellow/blue), the coherent motion direction was to the right (respectively to the left) in 80 % of the learning trials and the coherent motion direction was to the left (respectively to the right) in 20 % of the learning trials. For the remaining colour cue combination (e.g. yellow/yellow), the statistical bias was reversed. The coherent motion associated with a given cue condition in 80 % of the trials was named the Conditional Preferred Direction (CPD). The association rule, i.e. the statistical paring between colour combination and motion direction, was randomly chosen for each subject.
Data analysis

The subject response and the response times were separately analyzed for learning trials (30% coherence ratio) and for test trials (0% coherence ratio). For learning trials, as a significant proportion of dots move coherently in one direction, it was possible to compute the error percentage. For learning trials and for test trials with both colour cues, we also computed the percentage of response corresponding to the CPD and the mean response time. For test trials only, we also computed the percentage of response to the left (respectively to the right) for each of the following nine cue condition: the four combinations of two colours, the four combinations of one colour (blue or yellow in the upper area, blue or yellow in the lower area) and the single case with no colour cue at all.

These data have been used to adjust the parameters of the different probabilistic models (see below). The comparaison between experimental data in test trials and model prediction was based on the Kullback-Leibler divergence ($D_{KL}$).

For each subject $s$ and each test condition $i$, we computed the probability of observing a “left” response: $P(Left | i, s) = K_{is} / N_{is}$ where $N_{is}$ is the number of test trials and $K_{is}$ the number of left responses. Similarly, for each model $m$ and each condition $i$, we computed the the predicted probability of left response $Q(Left | i, m)$. The Kullback-Leibler divergence is defined as:

$$D_{KL}(is, i, s, m) = \frac{K_{is}}{N_{is}} \log\left[ \frac{K_{is}}{N_{is}Q(Left | i, m)} \right] + \frac{N_{is} - K_{is}}{N_{is}} \log\left[ \frac{N_{is} - K_{is}}{N_{is}(1 - Q(Left | i, m))} \right]$$

Finally, the score of a given model $m$ was computed as the weighted sum of the Kullback-Leibler divergence over all conditions and subjects:

$$D_{KL}(m) = \sum_{i, s} N_{is} \cdot D_{KL}(is, i, s, m)$$

Results

Subject responses with both colour cues

All subjects were able to detect the coherent motion quite accurately during the training phase. The mean error rate was 4.24 % (S.D.: 2.88 %) and ranged from 0 to 10.2 %.

Subject responses towards CPD in learning trials was close to the 80 % statistical bias (mean = 78.41 %, S.D. = 2.76 %). This result is a direct consequence of the subject ability to detect the coherent motion, so that subject responses logically reflect the statistical bias specified in the experimental procedure.

In test trials with both colour cues, subject responses were still biased towards CPD (mean = 58.95 %, S.D. = 12.03 %, range: 45 to 87.5 %). Since the bias has been computed from a total of 1012 test trials, it is largely significant for the set of subjects ($p<0.001$), though several individual subject results are not significant. No left/right bias was found, neither for the learning trials (mean left response = 49.54 %, N=1980), nor for test trials (mean left response = 49.90 %, N=1012).
Subject responses with missing cues

Because of the experimental procedure, each subject was submitted to a global bias in favor of CPD, independently of the colour combination: the coherent motion was towards CPD in 65% of learning trials and in the reverse direction in 35% of learning trials. Therefore, the subject responses in test trials with either partially missing or without colour cues can be also biased towards CPD.

Actually, half (8 among 16) of the subjects was submitted to a left CPD and gave a left response in 57.23% of the test trials without colour cues; similarly the other eight subjects were submitted to a right CPD and they gave a right response in 57.88% of the test trials without colour cues. So that, subject responses were biased towards CPD even when the conditioning colour cues were absent (mean =57.55 %, N=314, p<0.05). Subject responses were also biased towards CPD when only one colour cue was missing (mean=54.72 %, N=1046, p<0.02). Fig.2 summarizes the observed subjective bias towards CPD in the various experimental conditions.

Like in test trials with both colour cues, the range of individual response bias was quite large when one or both cues were missing: from 30 to 75% in test trail with one colour cue, and from 21 to 100% without colour cues. Though a significant bias towards CPD is obtained when all subject responses are pooled, this result should not mask the strong intersubject variability. All subjects have been submitted to the same training procedure (up to left/right, up/down and yellow/blue symmetry), but they might have stored different statistical correlations between colour combination and motion direction. To analyze these individual differences, it is necessary to precisely state and evaluate hypotheses about the way correlations were stored during the learning trials and exploited during the test trials. This type of analysis is detailed below.
Subject response times are plotted in Fig.3. In learning trials, the mean response time was 1101 ms (S.D.=419 ms), significantly shorter than the mean response time during the test trials with both colour cues (mean=1312 msec, S.D.=478 ms, paired t test = 2.73, p<0.05). In test trials without colour cues, the response time was also slightly increased as compared to test trials with both colour cues (mean response time: 1433 ms, S.D.=529 ms, paired t test = 2.40, p<0.05). However, in test trials with one missing cue, the response time did not differ significantly from the response time with both colour cues (mean response time =1320 ms, S.D.=492 ms). An increased response time is generally associated with an increase in task difficulty. As coherence ratio drops from 30 % to 0%, it sounds natural that subjects had more difficulty to report the perceived motion direction during test trials. As response time also increased when no colour cue was given to subjects, these results support the idea that the presence of colour cues helped subjects to perceive a global motion.

Models specification and comparison

To account for the observed experimental data, we built 5 probabilistic models, from simple to complex ones. Three of these models do not require the application of the marginalization rule, because the subject response can be directly predicted from a prior or a conditional prior. The remaining two models require the application of the marginalization rule. All models are based on four discrete variables: \( R \) is the predicted subject response (left or right), \( A \) and \( B \) are the colour cue values (blue or yellow) and \( C \) specifies the presence (or not) of the colour cues (none, up, down, both). All models can be viewed as particular (and simplified) cases of a generic model specified by the joint probability \( P(RA BC) \). Obviously, the complete generic model encompass all experimental conditions, so that it can exactly account for all observed subject responses.
Fig. 4: Cumulated $D_{KL}$ (ordinate, in bits) for all subjects obtained by the 5 models (see text for specification).

The simplest model (model 1) assumes that subject responses are not conditioned by the cue values and presence, i.e. it assumes that, as a result of the training, each subject has built a prior $P(R)$, eventually biased towards the CPD, but irrespective of the colour cue combination. This model is fully specified with one parameter, for instance $P(R = \text{Left})$, and this parameter can be easily evaluated by counting the number of “left” responses given by each subject in test trials. Model 1 does not need the marginalization rule, since the same prior distribution is applied when one or both colour cues are missing.

Models 2 and 3 assume that subject responses are conditioned by the cue values only in trials where both were present (i.e. when $C = \text{both}$). In model 2, the response probability is assumed to be the same for all other test trials, i.e. when one or both cues are missing. It is then specified by 5 parameters: the cue-dependent probabilities $P(R = \text{Left} | ABC = \text{both})$ and the remaining prior $P(R = \text{Left} | C \neq \text{both})$. In model 3, the response probability is supposed to depend on the cue presence variable, so that it requires 7 parameters: the four cue-dependent probabilities $P(R = \text{Left} | ABC = \text{both})$ and the three cue-independent priors $P(R = \text{Left} | C = \text{none}), P(R = \text{Left} | C = \text{up})$ and $P(R = \text{Left} | C = \text{down})$. The rationale of these models is that subjects have been able to build a cue-dependent probability during the training phase, when both cues were always present. If one or both cues are absent, they can only rely on a priori distribution. Again, models 2 and 3 do not require the application of the marginalization rule, since the prediction of subject responses is directly specified by the conditional forms.

Models 4 and 5 assume that the cue presence variable $C$ is not relevant to account for experimental data. When one (or both) cues is absent, the response probability is deduced by the application of the marginalization rule. Once the
joint probability $P(R A B)$ is defined, one can compute the response probability in each experimental condition as follows:

- both cues are present: $P(R | A B) = P(R A B) / \sum_R P(R A B)$
- the first cue is present: $P(R | A) = \sum_A P(R A B) / \sum_{R, A} P(R A B)$
- the second cue is present: $P(R | B) = \sum_B P(R A B) / \sum_{R, B} P(R A B)$
- both cues are absent: $P(R) = \sum_{A, B} P(R A B)$

Models 4 and 5 differ only by the way the joint distribution $P(R A B)$ is specified. In model 4, it is assumed that the colour cues are logically dependent on the motion direction, so that the joint distribution reduced to the product:


Model 5 assumes the reverse logical dependence between colour and movement, so that the joint distribution is equal defined as:

$$P(R A B) = P(R | A B).P(A B)$$

Model 4 requires 5 parameters to be specified: one for the prior $P(R)$ and two for each of the motion-dependent colour cue distribution. Model 5 requires 7 parameters to be specified: 3 for the cue combination probability $P(A B)$ and 4 for the cue-dependent motion distribution. Obviously, one can imagine other probabilistic models with an intermediate or smaller number of parameters. All these models require the application of the marginalization rule to operate on the experimental data. We restrained our analysis to model 4 and 5 because they are specified by the same number of parameters than models 2 and 3, respectively.

Note also that model 5 is a generic, in the sense that every other probabilistic model based on the 3 variables of interest ($R$, $A$ and $B$) is a particular case of model 5.

For each of the 16 subjects and each of the 5 models, we compute the optimal parameter set by first sampling the parametric space (number of samples 500000) and then with a gradient descent algorithm. As described in Methods, the optimality is defined in the sense of the Kullback-Leibler divergence between experimental data and model prediction. Fig.4 shows the cumulated score, i.e. the sum of optimal $D_{KL}$ over all subjects for each of the five models. While the simple model 1 works quite well for some subjects, it is systematically overmatched by the other models (see examples on Fig. 5). This strongly suggest that, at least for a significant proportion of participants, the perceived motion was biased towards a cue-dependent direction, as predicted by models 2 to 5. By comparing the score obtained by these models, it is also clear that the “marginalizing” models (4 and 5) perform globally better than the non-marginalizing models (2 and 3). Though the difference between the score of model 4 is only slightly better than the one of model 3, it should be recalled that model 4 is specified with less parameters (5 instead of 7). As model 4 is just a particular case of model 5, we expected to obtain for each subject an equal or a better score for model 5. Inspection of individual results show that the score improvement form model 4 to model 5 is inferior to 1 bit for 13 among
16 subjects. As a comparison, the score improvement from model 1 to model 4 is inferior to 1 bit for only 3 subjects, and from model 1 to model 5 for one single subject.

There is obviously a large variability among subjects, as the way the training phase has influenced their motion judgment in test trials. For may be 3 participants, the training results in a mere bias, explainable by a simple prior, irrespective of the conditional colour stimulus (an example is shown on Fig.5A). For the the majority of subjects, responses in test trials are far better explained by a marginalizing model (see Fig.5B for an example).

Fig.5: Percentage of left responses for two subjects, compared to the prediction of model 1 and model 5, for each colour cue combination. The symbol - stands for absence of one colour cue. Note that for one subject (top graphic)
the simple model 1 accounts reasonably well for almost all data. Larger discrepancies occur for the second subject (bottom), since model 1 cannot explain the noticeable incidence of cue-condition on perceived direction: see for instance the Blue/Blue trials and the -/Yellow trials.

Discussion

There are numerous adaptation mechanisms which allow living creatures to survive in spite of changing environments. These adaptation mechanisms occur at various speeds. For instance, the gain of vestibulo-ocular reflex can be adapted by the wearing of magnifying glasses within one hour or so (Collewijn et al, 1983), though the inversion of the reflex after continuous wearing of inverting goggles requires several days to be observed. Depending on the task difficulty, perceptive learning, generally assumed to improve the subject perceptive ability, is faster and less specific for easy tasks. As discussed by Ahissa & Hochstein (1997), easy task, fast learning and generalization capacity are characteristics of high-level visual processings (see also Hochstein & Alissa, 2002, for a review on reverse hierarchies in visual perception). Habituation is another example of adaptive mechanisms, in which repetitive or prolonged presentation of a given stimulus results in a decrease of the sensitivity to this stimulus.

Conditional learning departs from these two basic adaptation mechanisms. First, because there is no necessary improvement or decrease in sensitivity, but rather the appearance of a statistical bias in subjective responses which reflects a statistical correlation between a conditioning and a test stimulus. Though conditional learning has been demonstrated in animal behaviours since nearly a century, it is only recently that it has been shown also to occur in human perceptive judgements. Perceptual conditional learning develops quite fast, after one hundred of training trials or so (Haijang et al, 2006). In our experiment, we have also been able to observe a significant bias in perceptive judgment of most subjects after about one hundred training trials.

Owing to the particular design of our experimental procedure, we have investigated why kind of statistical information is stored during the training, and how it is exploited during the perceptive task. First, we have shown that subjects have not stored a mere bias, but a full description of statistical correlation between stimuli values, that is consistent with a joint probability distribution. The stored joint probability distribution might differ from the statistics specified in the experimental procedure. This is not surprising since the training correlation is not natural: there is no reason why the association of blue and yellow colours together with a global movement to the right should be more frequent in general. So that, it is very unlikely that subjects develop a very strong preference to perceive a figure moving to the right when the background is painted in blue and yellow.

Probability reasoning is based on two fundamental laws: the product law, often called Bayes’ theorem, and the additivity law, or marginalization rule (see Jaynes, 2003, for a detailed analysis). Up to now, all studies have focused on
the former, i.e. they showed how perceptive judgements are improved by a new observation, thanks to the multiplicative combination of prior and likelihood distributions. In the present study, we have shown that probabilistic reasoning, thanks to the marginalization rule, is also efficient in situations where cues are partially or totally missing.

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References


