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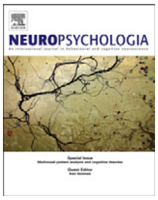

A preactivation account of sensory attenuation

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ABSTRACT

When humans perform actions that have a predictable effect in the environment, the intensity of these action–effects is attenuated. This phenomenon is thought to be related to motor based sensory prediction such that when the observed effect matches the prediction, the action–effect is attenuated. In the present paper we develop a new model to describe how this prediction might be implemented in the brain. This model supposes that voluntary action selection involves the preactivation of learnt action–effects. By modeling motor induced preactivation in sensory pathways we were able to generate a number of novel predictions regarding participants' performance in a contrast discrimination task. In order to test these predictions we trained participants to learn action–effect contingencies between left and right hand button presses and letter stimuli. We found a significant reduction in contrast discrimination sensitivity for stimuli that were congruent with these learnt action–effect associations. Furthermore, using participants' contrast ratings we were also able to show that this reduction in contrast sensitivity was driven by an increase in the internal response for lower contrast stimuli, consistent with the notion that sensory attenuation results from preactivation of learnt sensory action–effects. This provides a novel account of how motor prediction drives sensory attenuation of action–effects.

1. Introduction

Humans relentlessly interact with their environment, either reacting to external demands or producing desired effects in their surroundings. One of the theoretical pillars of research on action control is ideomotor theory (Greenwald, 1970; Hommel Musseler, Aschersleben, & Prinz, 2001; Lotze, 1852; Prinz, 1997). This theory is based on the fact that to act purposefully presupposes knowledge about action–effect relationships. It claims that performing an action results in a bidirectional association between the action and its ensuing sensory effect. Once acquired, these associations can be used to select an action by anticipating or internally activating their perceptual consequences (Greenwald, 1970; Prinz, 1990).

Anticipation of sensory effects as a principle of action control has also been embraced by computational approaches, in many of which forward models predict the future behavioral state of the system, and the sensory consequences of the given behavior (Wolpert, Ghahramani, & Jordan, 1995). Some accounts also include inverse models providing the motor command which, given the particular current state, would result in a desired sensory effect.

The notion of internal effect anticipation has been corroborated by a number of studies showing that action effects are processed differently when compared to stimuli that are externally triggered. Notably, it has been shown that voluntary actions result in attenuation of the action's sensory effect (Blakemore, Wolpert, & Frith, 1998), the notorious example being that it is difficult to tickle oneself. Sensory attenuation has been thought to result from efferent motor signals predicting the sensory consequences of the upcoming action. Predicted effect and actual sensory feedback are compared: if they correspond, the reafferences that have been anticipated are "canceled" (Bays & Wolpert, 2007a, b).

Sensory attenuation has primarily been studied as a neurophysiological phenomenon using EEG or fMRI to show attenuated cortical responses of self-produced stimuli (e.g., Bass, Jacobsen, & Schroger, 2008; Hughes & Waszak, 2011; Nagarajan, Aliu, & Houde, 2009; Schafer & Marcus, 1973). Comparatively few studies have investigated sensory attenuation by means of psychophysical methods. However, one of these studies tested whether internal action–effect anticipation genuinely alters the perception of the stimulus or whether it merely induces a response bias (Cardoso-Leite, Mamassian, Schutz-Bosbach, & Waszak, 2010).

According to signal detection theory (Green & Swets, 1966) a sensory process transforms the stimulus energy into an internal response (or representation) and a decision process decides on each trial whether or not to consider the stimulus to be present based on the current value of the internal response and the decision criterion. The difference in the mean and standard deviation of the distributions of internal responses elicited in trials in which the stimulus is physically present ("signal" distribution) vs. in which the

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stimulus is physically absent ("noise" distribution) characterizes sensitivity (d'). The higher the d' (i.e., the further apart the two distributions are), the better the perceptual system is able to differentiate signal from noise. The decision or response criterion (c) is the value that the internal response has to exceed in order for the participant to report the stimulus to be present. The lower c is the smaller the internal responses that the perceptual system still accepts as "stimulus present". Cardoso-Leite et al. (2010) assessed participants' detection performance to stimuli (tilted Gabor patches presented at detection threshold in 50% of the trials) in three different conditions: The stimuli were triggered by an action involving the internal anticipation of a learned visual effect that is either (1) congruent or (2) incongruent to the to-be-detected threshold stimulus, or (3) neutral. Using signal detection methodology (Green & Swets, 1966), Cardoso-Leite et al. were able to test for the influence of the congruency between anticipated and actual action effect on the detection of the latter, separately for sensitivity (d') and response criterion (c). They found that sensitivity (d') was reduced in the congruent condition compared to the neutral and incongruent conditions, reflecting sensory attenuation. At the same time the response criterion (c) was identical in the three conditions. This suggests that internal action–effect anticipation truly affects perception. That is, signal and noise distributions overlap more with than without internal effect anticipation.

But how, precisely, does internal effect anticipation result in larger overlap of signal and noise distributions? One possible scenario is that the signal distribution draws closer to the noise distribution because the anticipated sensory effect is inhibited (see Fig. 1, panel a). While many studies do not state a precise mechanism to explain sensory attenuation, some seem to reverberate the notion of a predictive inhibition as they state that the predicted effect is "subtracted" from the actual sensory effect or that the predicted effect is "canceled" (Bays, Flanagan, & Wolpert, 2006; Bays & Wolpert, 2007a,b; Blakemore et al., 1998). Revealing in this context is also the fact that the effect is usually called sensory suppression.

However, Waszak, Cardoso-Leite, and Hughes (2012) put forward a different scenario that can be directly derived from the ideomotor theory of action control (cf., Harless, 1861; James, 1890; Lotze, 1852) and, extending it, the common coding principle (e.g. Hommel et al., 2001; Prinz, 1997). The common coding principle claims that perception and action share a common representational code: actions are coded in terms of the distal perceptual effects they evoke in the environment. Consequently, perceiving an action effect involves the same representation as performing the associated action and, conversely, performing an action involves the same representation as perceiving the effect to which it is associated. In other words, performing an action results in the internal pre-activation of the sensory representation of the action's expected perceptual consequence. According to this scenario, internal action effect anticipation increases the mean level of activity in the network representing the expected effect to some pedestal level (see Fig. 1, panel b).

In terms of the signal detection theory, under this latter account the sensitivity loss for congruent action effects is due to discrimination of the signal activation from the pedestal level being more difficult than discrimination of the signal activation from the baseline level (e.g., in the incongruent and the neutral conditions of the study of Cardoso-Leite et al. (2010), in which baseline activity in the neurons coding the action effect is not raised to pedestal levels). That is, according to the preactivation account, sensitivity in congruent trials is reduced because the mean of the prestimulus activity distribution is increased, not because the mean of the signal distribution is decreased.

Possible support for this assumption comes from studies investigating the influence of sensory imagery on perception (for a detailed discussion of the possible overlap between preactivation and imagery see Waszak et al., 2012). For instance, Perky (1910) (also see recent replications by Craver-Lemley & Reeves, 1992) found that when participants were asked to imagine a particular object, they were less sensitive to the faint presentation of that object on the screen. As such, whether manipulated by the use of imagery or by motor induced preactivation, signal detection seems to be determined by the difference between baseline activation (when no stimulus is present) and the overall internal response driven by the signal.

To formalize this notion, we considered the shape of the neural response to stimulus intensity (or relative contrast) to be nonlinear and saturating (Albrecht, Farrar, & Hamilton, 1984; Dean, 1983; Ohzawa, Sclar, & Freeman, 1985; Saul & Cynader, 1989; see Fig. 2). This response is usually fitted by the hyperbolic ratio function (Heeger, 1992; Sclar, Ohzawa, & Freeman, 1985), $R = R_{max}(c^n/\sigma^n + c^n) + M$,[1] but in the current example we used a Weibull Repartition function, $F(x;k,\lambda) = 1 - e^{-(x/\lambda)^k}$, such as to avoid making any specific hypotheses regarding the maximum firing rate of a neuron or a population. In Fig. 2 the parameters λ and k were set to 10 and 1, respectively. In this function we considered x to be the neural entry and $F(x)$ the associated neural response. Furthermore this function appears to be a good fit of the visual system's response to stimulus contrast (Burr, Morrone, & Ross, 1994; Reynolds, Pasternak, & Desimone, 2000). Based on the idea that the neural firing rate is a function of the entry stimulation (McCulloch, 1943) we used this function as an integrator of the sum of the entry stimulation where $x = \sum_{i=1}^{n} x_i$, with i being the activation source. There are three possible activation sources: noise (n), stimulus contrast (c) or preactivation (p)). That is, the network is either activated by noise, internal preactivation and/or stimulus contrast.

As the noise baseline response function we took a spontaneous internal response activity (internal noise) of about 1% such that $x_{noise}(x_n)\,;\quad 1 - e^{-(x_n/10)^1} = 0.01$. This noise baseline is represented by the x-axis in Fig. 2. It reflects the network's mean activity when internal noise is the only source of neural activation. However, when a stimulus is presented, the neurons can be activated due to noise and the stimulus. The corresponding function $F(\sum_{i=1}^{n} x_i; 1,10) = 1 - e^{-(x_n + x_c/10)^1}$, thus, integrates stimulus activity and noise baseline activity (dashed function in Fig. 2). It represents the system's response to stimulus contrast without internal preactivation that is when it does not anticipate the stimulus represented by this particular set of neurons. In the case of internal preactivation, $x_{preactivation}(x_p)\,; 1 - e^{-(x_p/10)^1} = \omega$, the baseline is raised to a pedestal level (dashed horizontal line in Fig. 2). When a stimulus is presented in this situation, the neurons can be activated by noise, preactivation and the stimulus contrast. The corresponding neural response function $F(\sum_{i=1}^{n} x_i; 1,10) = 1 - e^{-(xc + xn + xp/10)^1}$ integrates stimulus contrast activity, noise baseline, and preactivation (solid function in Fig. 2). Note that the function is shifted upward resulting in stronger internal responses for identical stimulus contrasts as well as faster saturation of the internal response (i.e., saturation at a lower contrast values). Note also that the increase in internal response from the "without preactivation" (dashed line in Fig. 2) to the "with preactivation" function (solid line in Fig. 2) decreases with increasing level of activity. That is, the higher the activity level, the smaller the increase in internal response due to preactivation.

As noted earlier, according to Signal Detection Theory (SDT) *detection sensitivity*, as studied by Cardoso-Leite et al. (2010), is

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[1] Where R is the evoked response; R_{max} is the maximal attainable response; n is a constant exponent; c is the contrast of the test grating; σ^n is the semisaturation constant; M is the maintained discharge (Heeger, 1992).

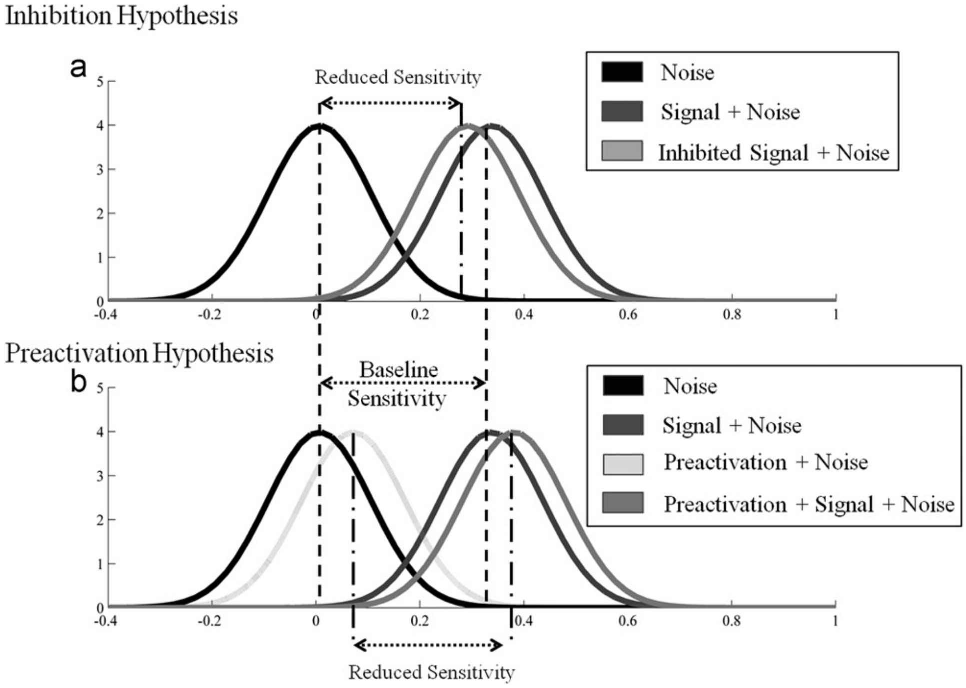

Fig. 1. Panel (a): illustration of the inhibition hypothesis where a correct prediction decreases the internal response of the signal (dashed to dash-dotted distribution). Panel (b): illustration of the preactivation hypothesis where the internal response increases more for the noise distribution (solid to dotted distribution) than for the stimulus distribution (dashed to dash-dotted distribution).

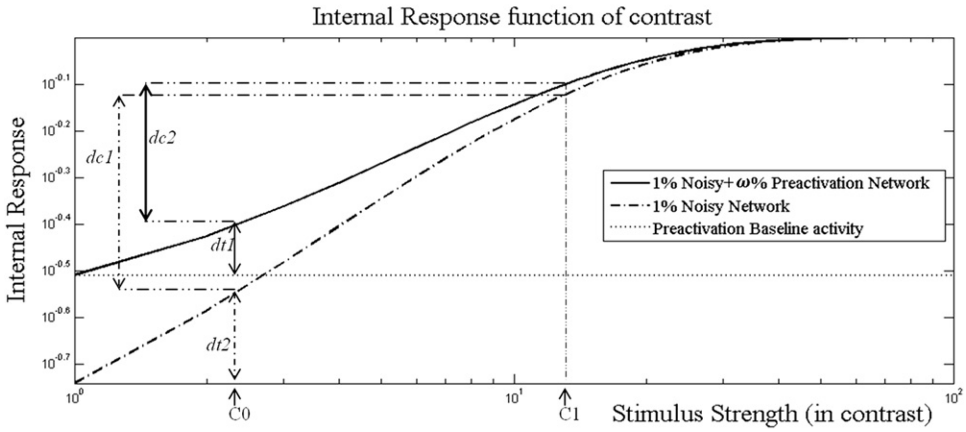

Fig. 2. Internal response as a function of contrast. *Sensitivity* is reflected in the distance between internal responses. C0: weak stimulus contrast; *dt1*: detection sensitivity when there is no preactivation; *dt2*: detection sensitivity when there is preactivation for the same stimulus (C0). The difference between $x_c = 0$ (baseline activity) and $x_c = C0$ is smaller with than without preactivation ($dt1 < dt2$) due to a smaller stimulus-driven increase of the internal response when there is preactivation than when there is not. C1: strong stimulus contrast; *dc1*: discrimination sensitivity between C0 and C1 when there is no preactivation; *dc2*: discrimination sensitivity between C0 and C1 when there is preactivation. The model predicts that, for any C0 and C1, discrimination is better without than with preactivation ($dc1 < dc2$).

represented by the difference between the baseline internal responses (in Fig. 2 the *x*-axis line when there is no preactivation and the dotted horizontal line when there is preactivation) and the internal response evoked by the stimulus added to the baseline. As we can see in Figs. 1b and 2 our model predicts this difference to be smaller when there is a preactivation in the network than when there is not. Hence our model predicts smaller sensitivity with than without preactivation due to a smaller stimulus-driven increase of the internal response when there is preactivation than when there is not (see detection *sensitivities* (*dt*) *dt1* and *dt2* for a stimulus of the same contrast (C0) in Fig. 2).

In addition to this predicted difference in detection sensitivity our model predicts that the *discrimination performance* between stimuli of two different contrasts should also be reduced in the presence of preactivation compared to without preactivation (see discrimination sensitivities (*dc*) *dc1* and *dc2* for two stimuli of different contrasts (C0 and C1) in Fig. 2). Furthermore, our model predicts that this reduced contrast discrimination for trials with preactivation should largely be driven by a change in the internal response of the weaker stimulus (stimulus C0 in Fig. 2), since at higher contrast values (stimulus C1 in Fig. 2), the difference between preactivation and no preactivation should be reduced or even abolished due to saturation. In contrast, cancellation accounts of sensory attenuation have been described such that "a cancellation mechanism that specifically affects self-generated input may nonetheless attenuate all self-generated input equally, irrespective of intensity" (Bays & Wolpert, 2007a,b, page 30 line 28). In such a scenario contrast discrimination should not be reduced, since the perceptual distance between the two stimuli should remain the same if cancellation affects stimuli of all intensity equally. In our model the reduced effect of preactivation on the internal response at high stimulus strength allows us to make a quite different prediction. As described above, discrimination sensitivity should be reduced since preactivation will influence the low contrast stimuli more than the high contrast stimuli. These basic features of our model are supported by a number of previous findings. First, neural saturation and the non-linearity of the neural response to intensity (Albrecht et al., 1984; Dean, 1983; Nieder & Miller, 2003; Ohzawa et al., 1985; Saul & Cynader, 1989) suggest that a linear increase in intensity translates to a non linear log-like increase in neural response. As such, an incremental increase in stimulus intensity will result in smaller increases in the neural response as intensity increases. Second perception of intensities has been seen to follow a Weber–Fechner law (Dehaene, 2003 for numerosity; Gorea & Sagi, 2001 for contrast) meaning that a given increase in stimulus energy will affect perception more if the stimulus is weak. Taken together these findings provide strong support for the basis of our experimental prediction, namely that a fixed amount of stimulus preactivation will influence the internal response to a greater degree for low contrast than for high contrast stimuli.

We tested these predictions by asking participants to perform a contrast discrimination task for stimuli that were congruent (trials where the preactivation matches the stimulus) or incongruent (trials where the preactivation does not match the stimulus) with previously learnt action effect associations. Participants performed left- or right-hand voluntary actions on each trial that had previously been associated with the letters A and H respectively. In the test phase these stimuli were presented at one of the two contrast values (C0 or C1) and participants were required to report the perceived contrast at the end of each trial on a 100 point scale, where ratings of below 50 were classed as C0 and ratings above 50 as C1. According to our model, congruent trials should result in reduced contrast discrimination compared to incongruent trials, with this difference largely determined by changes in the internal response for the weaker stimulus.

2. Materials and methods

2.1. Stimuli

Experimental stimuli were generated and presented with Matlab 2007b using the psychophysics toolbox (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997). The stimuli were two white letters (A and H) displayed on a 15 in. CRT monitor at a 60 Hz refresh rate and fitted into a virtual square of 2.9° of visual angle. The screen resolution was set at 800 × 600 pixels. These two stimuli were presented at two different contrast values (C0 and C1; see contrast determination phase) at the center of the screen. In the test phase we used a uniform noise texture to increase perceptual variance. This noise was a 100 × 100 matrix filled with an equal number of white and black pixels. The matrix was re-sampled (using the randperm function in Matlab) on each screen refresh. The mean luminance of the noise was then equal to the gray background.

2.2. Contrast determination phase

In order to determine individual contrast values C0 and C1 yielding a discrimination d' of about 2, every participant completed a psychophysical staircase converging on 90% correct responses in a letter identification task (A vs. H). We employed an adaptive staircase to manipulate stimulus transparency using an accelerated stochastic approximation algorithm as described by Kesten (1958). The initial step size was 20 and we stopped the staircase when the step size was 1 (in transparency). The correct response rate was used to ensure that the stimuli were supraliminal and that we could then independently manipulate discrimination. We used this contrast value as the referential contrast C0 in a 2AFC paradigm (with constant stimuli ranging from C0 to C0 + 12%) in order to calculate, the contrast value of C1 yielding 85% correct responses in a luminance discrimination task (C0 vs. C1). For an ideal observer, this contrast yields a discrimination d' of around 2 (Macmillan & Creelman, 1991). Pilot experiments showed this procedure to work reliably.

2.3. Association phase

Participants fixated on a 3.3° visual angle square located at the center of the screen. They were asked to press with their right/left index finger one of the two keys (P and A on a standard French (AZERTY) keyboard), each key press triggering presentation of a visual effect (A or H). The key-letter mapping was counterbalanced across participants. The letters appeared 100 ms after the key press at full contrast in the square at the center of the screen.

There were two types of association phase. First, in the free association ("FreeAsso") blocks the action sequence (left/right) was freely generate by the participants at a pace of about 1 key press every seconds for 50 s. In 5% of the trials the visual effect was a W. In these catch trials, the participant had to press both buttons within 1 s of the appearance of the stimulus. Catch trials were meant to ensure that participants paid attention to the effect stimuli. Second, in memory association blocks ("MemoryAsso") random lists of As and Hs were presented to the participants (the average list size was 5). The lists were presented via headphones as spoken letters. After the lists were presented, participants had to reproduce the sequence by pressing the corresponding button sequence.

The association phase consisted of three FreeAsso blocks and two MemoryAsso blocks. Each FreeAsso block contained 50 trials. Each MemoryAsso block contained 30 sequences of, on average, five items. Each participant ran three FreeAsso and two MemoryAsso blocks.

2.4. Test phase

Participants fixated a square at the center of the screen, just as in the association phase. They were asked to produce, at random, right and left key presses. Again, the key presses triggered presentation of letter stimuli 100 ms after the key press for a duration of 200 ms. In this phase, however, Hs and As were presented randomly after each key press, such that 50% of the generated stimuli were congruent with the previous association (i.e., the letter corresponded to the one associated to that key press in the association phase), and 50% were incongruent. The stimuli appeared randomly (but in equal proportions) with the luminance C0 or the luminance C1. Participants were told that there were two categories of luminance ranging from the value 0 to 50 for the C0 category and from 50 to 100 for the C1 category. In order to maintain this uncertainty about the contrast on 5% of the trial stimuli appeared with a random contrast between C0 − 15% contrast and C1 + 15% contrast. After the stimulus had disappeared participants were required to judge the luminance value of the stimulus on a luminance response bar. On this bar participants could place the cursor on the perceived contrast value (from 0 to 100 except 50) with values under 50 corresponding to C0 and over 50 corresponding to C1. Participants completed three tests blocks of 44 trials before being in a re-association phase composed by one of each association blocks and ran three others tests blocks. In total participants responded to 264 test trials.

2.5. Participants

Fifteen participants took part in the experiment. They were naive to the purpose of the experiment. Three of these 15 participants were excluded from the analysis as their luminance discrimination d's were almost 0 (mean $d'=0.038$ SEM = 0.124). Six of the remaining participants (seven women, five men; mean age = 24 years, SEM = 3.69 years) had action–effect mapping 1 (left → A, right → B), and six had mapping 2.

2.6. Analysis of discrimination performance

The luminance discrimination task was considered to be a yes/no protocol, with C1 being the target. That is, a C1 response to a C1 stimulus is a hit, a C1 response to a C0 stimulus is a false alarm, etc. d' and c are calculated using $d'=z(\text{hit rate}) - z(\text{false alarm rate})$ and $c=-0.5\times[z(\text{hit rate})+z(\text{false alarm rate})])$.[2] d' and c were calculated separately for congruent and incongruent trials.

3. Results

We first analyzed our data dependent on participants' contrast discrimination, such that we divided our contrast rating into two classes of contrasts (corresponding to C0 and C1). Discrimination performance (d') was lower in the congruent condition than in the incongruent condition (congruent: $M=1.82$, SEM = 0.54; incongruent: $M=1.98$, SEM = 0.59). A repeated measure one factor ANOVA with

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[2] z being the inverse normal law $f(x;\mu,\lambda)=[\lambda/2\pi x^3]^{1/2}\exp((-\lambda(x-\mu)^2/2\mu^2 x)$.

the factor of congruency (congruent vs. incongruent) showed that this effect of congruency on d' was significant ($F(1,11)=5.59$, $p=0.037$). At the same time, the criterion was not different in the two congruency conditions (congruent: $M=0.32$, SEM$=0.23$; incongruent: $M=0.34$, SEM$=0.33$; $F(1,11)=0.15$, $p=0.69$).

We performed separate repeated measure ANOVAs for response side (left vs. right) $*$ congruency (congruent vs. incongruent) and for mapping group (group 1 vs. group 2) $*$ congruency (congruent vs. incongruent). Both ANOVAs showed the congruency effect to be identical for both response sides and for both mapping groups (interactions: $F(1,11)=0.99$, $p=0.33$ and $F(1,5)=0.064$, $p=0.81$, respectively). Taken together, these findings support the hypothesis that preactivation of predicted action–effects reduces discrimination sensitivity.

Since participants provided their judgments of contrast using a continuous scale from 1 to 100 this allowed us to analyze not only their overall contrast judgment (C0 or C1) but also their rating of the perceived intensity (contrast) of the stimulus. We used these ratings to compute ROC (receiver operating characteristic) curves for each participant. We calculated the area under the curve ($A'=1/2*\Sigma(F_{i+1}-F_i)(H_{i+1}+H_i)$) separately for every participant and condition. A one-tailed t-test revealed a near significant difference such that incongruent trials were perceived as being of higher contrast that congruent trials (congruent: $M=0.871$, SEM$=0.05$; incongruent: $M=0.88$, SEM$=0.06$; $t(11)=0.8866$, $p=0.0515$). As we can see in Fig. 3, the individual values of A' are in majority above the equality line (Cong=Incong). The same holds for d' (see Fig. 3).

Our final analysis aimed to test the prediction that the difference in contrast discrimination described above is driven by an increase in the internal response for incongruent trials with preactivation. Type 2 SDT states that participants' ratings are highly correlated with their internal response and are commonly used to study perceptual awareness (Galvin, Podd, Drga, & Whitmore, 2003; Kunimoto, Miller, & Pashler, 2001; Sergent & Dehaene, 2004). Thus, we used the perceptual report of our participants to estimate the shapes of the internal response of the participants. By binning the participants' answers on the visibility scale we obtained an approximation of the distribution evoked by C0 and C1 in both conditions (Fig. 4).

A repeated measure ANOVA with the factor congruency and contrast revealed no differences in variance between the responses distributions ($C0_{\text{congruent}}$: mean: 16.8, SEM: 2.8; $C0_{\text{incongruent}}$: mean: 16.5, SEM: 3.2; $C1_{\text{congruent}}$: mean: 17.3, SEM: 3.9; $C1_{\text{incongruent}}$: mean: 17.7, SEM: 3.1, $F(3, 33)=0.9$, $p=0.45$). As regards the mean responses a repeated measures ANOVA including the factor of contrast and congruency revealed a significant effect of contrast ($F(1,11)=122.8$, $p<0.0001$), no effect of congruency ($F(1,11)=0.1$, $p=0.73$) and a nearly significant interaction effect ($F(1,11)=4.6$, $p=0.054$). A one-tailed t-test comparing the mean of C0 for congruent and incongruent trial showed internal response of C0 to be larger for congruent than for incongruent trials ($C0_{\text{congruent}}$: mean: 28.50, SEM: 5.39; $C0_{\text{incongruent}}$: mean: 27.01, SEM: 4.89; $t(11)=1.71$, $p=0.05$). The internal response of C1, by contrast, did not differ significantly between congruent and incongruent trials ($C1_{\text{congruent}}$: mean: 58.68, SEM: 6.77; $C1_{\text{incongruent}}$: mean: 59.44, SEM: 9.55; $t(11)=-0.54$, $p=0.29$). Regarding the individual data (Table 1) this effect appears to be confirmed by the fact that the difference between congruent and incongruent is doubled for C0 compared to C1. This pattern of results is just what our model predicts, if the activity level of C1 is already nearly saturated.

4. Discussion

We trained participants to acquire associations between left- and right-hand key presses and the visual presentation of the letters A and H, respectively. In a subsequent test phase, participants performed right- and left-hand key presses that triggered the presentation of either a H or an A. The letters appeared in one of the two contrasts (C0/C1). The stimulus could either be congruent or incongruent with respect to the learnt action–effect contingency. We showed that luminance discrimination between the two contrasts yielded a smaller d' for congruent action–letter combinations (i.e., when the letter corresponded to the one associated to that key press in the association phase) than for incongruent combinations. Subsequent analysis of participants' luminance ratings showed that this reduction in d' was due to internal responses of C0 being increased for congruent compared to incongruent trials, while internal responses of C1 not being different for congruent and incongruent trials. This brings about that the internal responses of C0 and C1 are drawn together for congruent compared to incongruent trials, making the luminance discrimination more difficult in the former than in the latter type of trial. Note that this pattern of results corresponds to what the preactivation account outlined above predicts. The account predicts a reduced contrast discrimination performance for congruent compared to incongruent stimuli, because the stimulus-driven internal response gain is lower with than without preactivation. The stronger the stimulus the smaller the increase of the internal response due to the preactivation [i.e., with preactivation (congruent) compared to without preactivation (incongruent)]. The presence of a shift of the internal response for C0 but not for C1 in our data confirms the model's prediction.

In order to estimate the level of preactivation that would result in a difference in discrimination d' between a situation without and a situation with preactivation as observed in our experiment, we attempted to use our model to recreate our observed results. We first fitted the exact discrimination d' we observed in the incongruent condition with a Weinbull function, using the contrast values from our experiment C0 (36%) and C1 (51%). To be able to calculate d' (distance of the distributions/variance of the distributions) we needed to estimate the variance of the internal response of a given contrast. Since the variance of the participants' perceived contrast ratings did not differ between our conditions any variance satisfying the constraint of returning the exact experimental d' could be chosen. Moreover, we constrained the function to minimize the differences in internal response to C1 across all possible preactivation levels. We found that, with a Weibull repartition function having the parameters $\lambda=14.8$ and $k=1$ we were able to fit a 3% variance of the internal response to yield exactly to the observed d' for incongruent trials (1.98). The internal responses for C0 and C1 were 90.7% and 96.6%, respectively. This fits well the fact that our stimuli were highly supraliminal (see Methods and materials section).

Using the function for the incongruent condition as a starting point, we estimated the level of preactivation necessary to yield a d' reduction as observed in the experiment. We found that a preactivation activity of 8% was sufficient to reduce d' from 1.98 in the incongruent condition to 1.82 in the congruent condition. The internal responses to C0 and C1 in the latter condition were 91.4% and 96.9%. Hence, the internal response for C0 increased much more (0.7%) than the internal response of C1 (0.3%), replicating what we observed in our experimental data.

To further validate our model, we assessed whether the same amount of preactivation would explain the decrease in detection d' observed by Cardoso-Leite et al. (2010). In a detection task sensitivity is represented by the distance between the mean baseline internal activity ('noise') and the mean internal activity driven by the stimulus ('signal'+'noise'; see Figs. 1 and 2a). Cardoso et al. observed a reduction in detection d' from the incongruent condition (2.55) to the congruent condition (2.37). We modeled detection d' as the difference in internal response

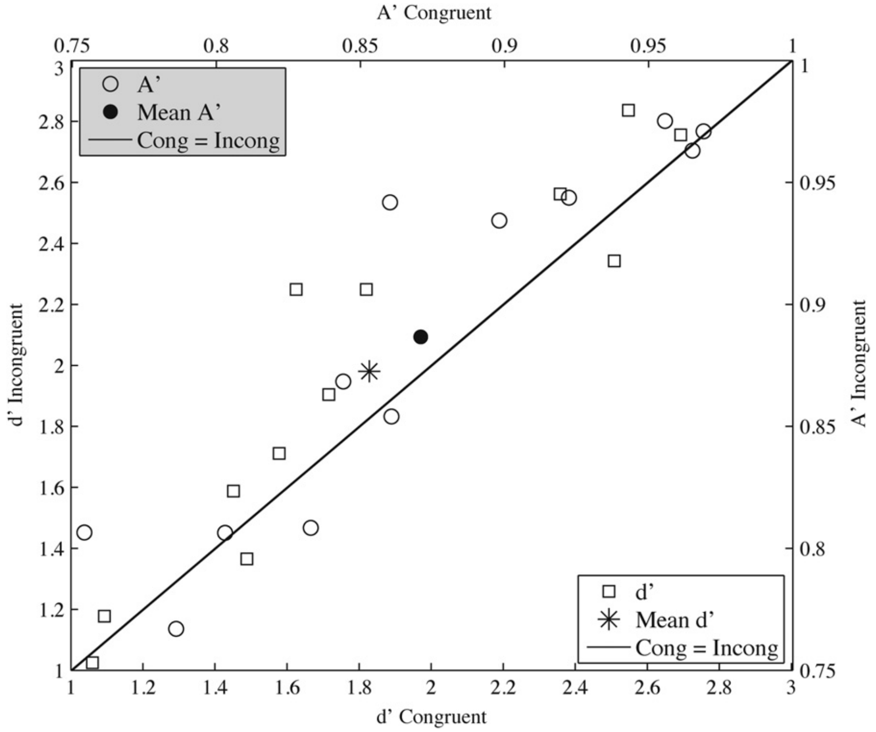

Fig. 3. Individual results for *d′* and *A′*. The *x*-axis represents the individual values for congruent trials (*d′* on bottom *x*-axis, *A′* on top *x*-axis). The *y*-axis represents the individual values for incongruent trials (*d′* on left *y*-axis, *A′* on right *y*-axis). As we can see the participant results are mostly distributed above the equality line (Cong=Incong) indicating that for the vast majority of subjects *d′* and *A′* were better in the incongruent than the congruent condition.

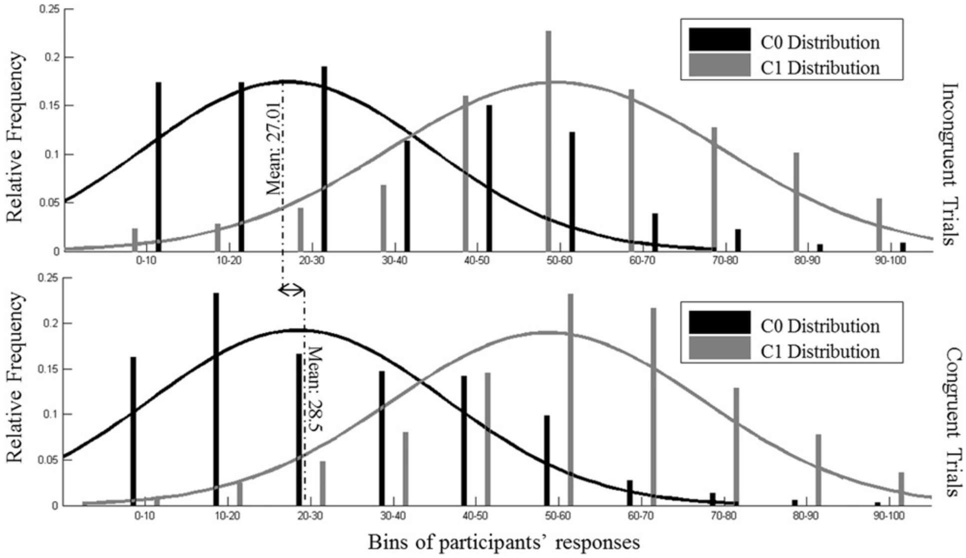

Fig. 4. Frequencies of participants' visibility rating fitted with a Gaussian distribution. Panel (a): incongruent trials (without preactivation). Panel (b): congruent trials (with preactivation). The mean of the distribution of the internal responses for C0 is higher when there is preactivation than when there is not, resulting in a decrease in discrimination sensitivity between C0 and C1.

Table 1
Individual ratings for both contrast value and both condition (congruent and incongruent).

	Participant	1	2	3	4	5	6	7	8	9	10	11	12	Mean
Subjective response L0	Congruent (C)	17.05	27.25	29.13	30.20	31.30	31.32	32.52	29.30	32.10	35.47	27.37	19.05	28.50
	Incongruent (I)	19.93	25.87	27.23	30.70	29.75	32.22	30.40	29.37	29.95	26.20	27.25	15.28	27.01
	C−I	−2.88	1.38	1.90	−0.50	1.55	−0.90	2.12	−0.07	2.15	9.27	0.12	3.77	1.49
Subjective response L1	Congruent (C)	66.75	69.45	48.93	68.18	60.62	55.93	61.82	51.55	57.20	55.65	51.52	56.58	58.68
	Incongruent (I)	69.70	70.97	49.98	77.92	55.02	56.48	67.47	52.95	56.57	48.13	55.70	52.40	59.44
	C−I	−2.95	−1.52	−1.05	−9.73	5.60	−0.55	−5.65	−1.40	0.63	7.52	−4.18	4.18	−0.76

between the baseline activity corresponding to 1% of internal activity due to noise and the internal response to a stimulus at threshold (9% of internal activity yielding a detection d' of 2.55). We found that adding 8% of preactivation activity (as estimated above) made detection d' drop to 2.34. Hence, the same preactivation level of 8% could also explain the results from Cardoso-Leite et al. (2010).[3]

The preactivation account described above fits also very well to recent findings from experiments on action effect anticipation using neurophysiological methods. Kuhn, Seurinck, Fias, and Waszak (2010) harnessed the modularity of perceptual category representation in the human brain to assess action-induced activity in areas involved in the perception of particular classes of stimuli. They made participants acquire an association between left and right button presses and face and house stimuli, respectively, as action effects. During the test phase, participants continued to make left- and right-hand responses but no action–effects were presented. Nonetheless, they observed that activity in fusiform face area (FFA, which shows selective activation for faces, e.g. Kanwisher, McDermott, & Chun, 1997) was increased for actions associated to face stimuli, whereas activity in the parahippocampal place area (PPA, which shows selective activation for places, e.g. Epstein & Kanwisher, 1998) was increased for actions associated to house stimuli. Note that these activations were observed in the absence of any visual stimulation. It is thus the action itself that induces activity in FFA and PPA. The results thus demonstrate that performing an action entails activity in perceptual areas as if the anticipated sensory action effect is actually perceived, corroborating the notion of action-induced preactivation in perceptual networks representing the expected sensory effects (for a review of functional and neurophysiological mechanisms of effect anticipation see Waszak et al., 2012).

In the present paper we introduce a new preactivation-based model to account for the role of motor prediction in sensory attenuation. This model allowed us to derive a number of novel hypotheses regarding participants contrast discrimination performance as well as the precise effect of preactivation on their internal response. We should note such preactivation induced sensory attention might not be limited to action prediction, but may also result from other non-motor prediction mechanisms (see Hughes, Desantis, & Waszak, 2013 for a discussion). Indeed, parallels may also be drawn between sensory attenuation and the decrease in neural responses observed to result from stimulus repetition (Grill-Spector, Henson, & Martin, 2006; Henson, 2003; Wiggs & Martin, 1998) or sensory imagery sensory imagery (Perky, 1910; see Waszak et al., 2012 for a more detailed discussion). Our experimental findings confirmed the predictions of the model. Furthermore, the current model not only successfully generated testable predictions for the present experiment, but also explained the reduction is stimulus discrimination previously observed for accurately predicted action–effects (Cardoso-Leite et al., 2010). This model thus provides a novel way to understand the way in which predictive action mechanisms lead to changes in the way we perceive the effects of our actions.

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[3] Note that we did not use the experimental contrast of the study of Cardoso-Leite et al., but rather, for the sake of simplicity, we used contrast values that would yield the d' values observed in the study from Cardoso-Leite et al., given the functions fitted above.

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