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ERP and behavioral evidence of increased sensory attenuation for fear related action outcomes.

Running title: Sensory attenuation for fearful faces.

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Highlights

- Increased sensory attenuation for fearful compared to neutral faces.
- Neurophysiological attenuation for predicted fearful faces only.
- Enhanced subjective fear ratings for congruent fearful faces.

**Abstract**

Voluntary action selection entails the representation of the expected consequences of the action. Previous evidence suggests that accurate action-effect prediction modulates both ERP and behavioural markers of sensory processing – a phenomenon known as sensory attenuation. This may play an important role in monitoring the success or failure of our actions, or attributing agency. Nonetheless, the vast majority of studies in this domain focus on simplistic visual and auditory stimuli. Given that we rarely perform voluntary actions with the aim of generating such stimuli in social contexts, this provides little indication of the extent to which sensory attenuation operates in everyday behavior. The present study investigated ERP and behavioral measures of sensory attenuation for fearful and neutral facial expressions. Participants were trained to associate one voluntary action with the presentation of a fearful face, and another action with a neutral face. We measured both ERP responses and behavioural ratings following presentation of faces whose emotional content was either consistent or inconsistent with the action prediction. We observed significant modulation for fearful outcomes only, suggesting that sensory attenuation is heightened to stimuli of high social relevance. The N170 response was significantly attenuated for congruent fearful faces, but not for congruent neutral faces (in comparison to incongruent faces). Similarly, behavioral ratings were modulated only for fearful faces but not neutral faces. This provides new insight into how social and affective outcomes modulate sensory attenuation and may have implications for implicit sense of agency for socially relevant stimuli.

Keywords: Agency; Sensory Attenuation; Motor Prediction; Event-Related Potentials; Face Processing.

## Introduction

Sensory attenuation refers to the fact that the effects of one's voluntary actions exhibit a reduced neural response. This may play an important role in monitoring the success or failure of our actions, or attributing agency. The present study investigated whether the processing of predicted sensory action effects is modulated by their affective content. This provides important new insight in to the role of motor prediction in perception for socially relevant stimuli.

The majority of recent research on sensory attenuation has focused on processing of simple auditory, and, to a lesser degree, visual stimuli that follow voluntary action effects (for recent reviews see Hughes, Desantis, & Waszak, 2013b; Waszak, Cardoso-Leite, & Hughes, 2012). These studies have shown that self-triggered tones exhibit reduced auditory (Baess, Jacobsen, & Schroger, 2008) and visual (Hughes & Waszak, 2011) ERP responses compared to externally triggered stimuli. Other researchers have manipulated the degree to which the observed action effect is congruent with a particular action (Cardoso-Leite et al., 2010; Hughes, Desantis, & Waszak, 2013a; Roussel, Hughes, & Waszak, 2013, 2014), or whether actions are consistent with unconscious primes (Stenner et al., 2014). These studies have shown reduced early visual (Roussel et al., 2014) and auditory (Hughes et al., 2013a) ERP responses to congruent action effects, as well as reduced luminance discrimination (Roussel et al., 2013, 2014) and target detection (Cardoso-Leite et al., 2010).

Taken together, these findings suggest that sensory events that are predicted by one's voluntary actions are processed very differently to unpredicted stimuli. The present study investigated both neurophysiological and behavioral responses to fearful and neutral faces, to provide new insight in to the degree to which sensory attenuation might be modulated by these social and affective stimuli. The present study assessed whether sensory attenuation might differ dependent on the emotional content of voluntary action effects. Since faces are

crucial for communication and social interaction, they are an ideal stimulus to measure the role of emotion on the sense of agency. One previous study (Hughes & Waszak, 2014) provided preliminary evidence of the efficacy of such ecologically valid stimuli in generating neurophysiological attenuation. However, that study focused only on neutral faces and houses, and did not incorporate a behavioral measure of sensory processing. In the current study, participants were trained to associate one of two buttons with the presentation of a fearful face, and the other button with a neutral face. Occasional violation of this pattern allowed for the assessment of the influence of action prediction on emotion processing in faces. Following the presentation of the face, participants were asked to rate the amount of fear presented in the face. This behavioral index differs significantly from those previously employed, which either use subjective ratings of intensity (Blakemore, Frith, & Wolpert, 1999; Roussel et al., 2013, 2014) or psychophysical measures such as stimulus detection (Cardoso-Leite et al., 2010) or point of subjective equality (Sato, 2008; Stenner et al., 2014). In contrast, participants were asked to provide a rating based on the emotional content of the visual stimulus rather than its physical strength. This provides novel insight into how action prediction modulates the processing of the content of action effects.

The absence of sensory suppression in patients suffering from hallucinations (Blakemore, Wolpert, & Frith, 2000) has been taken as evidence for the role of this phenomenon in self-monitoring and sense of agency (Frith, 2012; Frith, Blakemore, & Wolpert, 2000). Recent evidence from the intentional binding paradigm (Takahata et al., 2012; Yoshie & Haggard, 2013) point to the possibility that pre-reflexive agency is increased for positively valenced stimuli. Therefore, the current study also aims to provide further evidence about the role of emotion in sense of agency.

Previous research on sensory attenuation with simple visual and auditory stimuli has observed reduced auditory N1 amplitude (Baess et al., 2008; Hughes et al., 2013a), or

primary visual responses (Roussel et al., 2014). Therefore, we might expect to observe attenuation in the visual P1 response. However, one previous study using neutral faces and houses (Hughes & Waszak, 2014) observed attenuation only in later components, suggesting that accurate prediction of higher-level visual features results in modulation of later stages of sensory processing. Of particular interest for the present study are the N170 component, and the later P2 component. The N170 ERP component is reliably observed following face stimuli (Bentin et al., 1996) and has been seen to be modulated by emotional content of the face (Batty & Taylor, 2003; Blau et al., 2007), such that a greater N170 is observed for fearful faces. Other studies have shown that later components are modulated by both emotion (Eimer & Holmes, 2002) and facial recognition (Gosling & Eimer, 2011). Hughes & Waszak (2014) observed modulation only in the positive peak (P2) immediately following the N170 as a function of motor prediction.

Given that the P1 component is not typically modulated by the emotional content of a face (Eimer & Holmes, 2002) and that previous research observed no attenuation of P1 for predicted faces (Hughes & Wasak, 2014), modulation of this component in the present study would be unlikely. Rather, we predicted that we would observe modulation the N170 component for fearful versus neutral faces in this present study, with a larger N170 for fearful faces. Importantly, this should also be modulated as a function of action effect congruency, such that the N170 should be more typically fearful (greater) for incongruent fearful faces, compared to congruent fearful faces. This would reflect attenuation of the N170 response to a fearful face. Precise predictions in the P2 time range are more difficult to establish, with previous research reporting either sustained positive (Eimer & Holmes, 2002) or negative components (Gosling & Eimer, 2011), or more focal modulations (Hughes & Waszak, 2014). Nonetheless, given previous reports of prediction related differences in this time range using

a similar paradigm (Hughes & Waszak, 2014), we predicted some modulation of the P2 component.

## **Methods**

### *Participants*

Data was collected from 28 volunteers. All participants were right-handed, had normal or corrected-to-normal vision, and had no history of epilepsy. Individuals who were taking psychoactive drugs were excluded from participating. One participant withdrew partway through the experiment. One participant was excluded from the analysis as they exclusively pressed the left key, leaving no trials in two of the experimental conditions. Three further participants were excluded due to technical problems with the EEG recording, leaving 23 participants (14 female and 9 male), with a mean age of 22 years and 10 months (range 19 to 30 yrs). All participants signed an informed consent prior to the experimental session, and were free to withdraw at any point. The study was approved by the University of Essex ethics committee, and was performed in accordance with the declaration of Helsinki.

### *Experimental Procedure*

The experiment was conducted using Matlab (MathWorks) with the psychophysics toolbox (Brainard, 1997), with stimuli presented on a 21 inch monitor, 60 cm from the participant. The experimental session began with a series of practice tasks, which were designed to familiarize participants with the task as well as to allow participants to build up the action effect contingencies. In the first practice task (association phase) participants were asked to press either the k, or the l key on a keyboard, with their right hand. They were free to choose which button to press on each trial, and when to press the button, with the exception that they should not perform the action until at least 500 ms after the start of the trial (the

onset of the fixation cross). If participants pressed too quickly then a red fixation cross would appear for 200 ms, before the trial was restarted (following a random inter trial interval and then a white fixation cross). Following each valid button press, a blank screen was presented for 200 ms, and then an image of a face appeared. This face could be either a face with a neutral expression, or a face with a fearful expression. One button press (k or l) always led to one expression (fear or neutral), and the other button was followed by presentation of the other expression. 10 Neutral and 10 fearful faces were used in the experiment, taken from a standard set of affective face stimuli (Ekman & Friesen, 1976). The stimuli were presented in the center of the screen and measured 6.5 x 4.5 cm and were presented for 200 ms.

Following the presentation of the face, separated by a blank screen of 1 to 1.5 s, participants were asked to rate the amount of fear present in the facial expression. Participants moved a cursor up and down to indicate the amount of fear present in the face. The word “Fear” was presented above the bar, and “No Fear” below the bar. To the right of the bar a number from 1 to 100 was presented (see Figure 1). The bar started in a random position on each trial. To move the bar up and down, participants pressed the d and c keys respectively. As the bar moved the number to the right also increased or decreased. When participants were happy with their answer they pressed the space bar to confirm. An inter-trial interval of 1-1.5 seconds separated each trial. This first practice task consisted of 30 trials.

In the second practice task (memory phase) participants were presented with a sequence of the words “Fear” and “No Fear”. The first sequence contained 4 stimuli (2 of each type), presented in a random order. Following the presentation of the words, participants were required to press the appropriate buttons to recreate the sequence. Following a correct sequence 1 stimulus was added to the newly randomized sequence (up to a maximum of 7



stimuli). If participants failed to successfully replicate the sequence, 1 stimulus was removed (down to a minimum of 3 stimuli). Participants received feedback after each response sequence to inform them of their accuracy. This practice task contained a total of 10 sequences. If participants failed to replicate at least 6 out of the 10 sequences, they were asked to repeat the task to ensure that they had adequately learnt the action-stimulus contingencies. As in previous studies (Hughes & Waskak, 2014; Roussel et al., 2013; 2014), the memory phase was included to reinforce the action-effect contingencies.

Following these practice tasks, the participants were fitted with the EEG recording apparatus. They then completed 4 sequences of the association phase, the memory phase, and the test phase. The association phase consisted of 20 trials, and the memory phase of 5 sequences. The test phase was identical to the association phase, except that in 25% of trials the expected action effect relationship was violated. For instance, if a participant had learnt that the left button actions always led to a fearful face, then on 25% of trials in the test phase left button presses would result in the presentation of a neutral face rather than a fearful face. These will henceforth be referred to as incongruent trials, with consistent mappings referred to as congruent trials. Each block consisted of a minimum of 80 trials. The block terminated once participants had pressed each button on 40 trials, up to a maximum of 140 trials in the block. This was to ensure that they were presented with each face stimulus once in the incongruent conditions. As in the acquisition blocks, participants were required to rate the amount of fear depicted in the face on each trial. See Figure 1 for the trial timeline during the test phase.

#### *EEG recording and data analysis*

Electroencephalography (EEG) data were recorded from 31 scalp locations using a Brain Vision ActiCHamp system using the modified combinatorial nomenclature electrode placements, relative to a nose tip reference. The EEG was digitized at 500 Hz. Analysis was

conducted using EEGLab (Delorme & Makeig, 2004) and custom-built Matlab scripts. The data were re-sampled offline to a 250 Hz sample rate, and low-pass filtered at 40Hz. Epochs were generated from -1000 to 1000 ms relative to the onset of the face stimulus; with action onset at -200 ms. Baseline correction was applied from -200 to 0 ms.

Initial artifact rejection was conducted in a semi-automatic manner (in EEGLab) by rejecting epochs with improbable data and abnormally distributed data, where the threshold in each case was set to 5 standard deviations. Noisy channels were rejected by visual inspection and marked for later removal and later interpolation (see below). Ocular artifact correction was conducted in EEGLab in Matlab using independent component analysis (Delorme & Makeig, 2004). Following removal of eye blinks and eye movements, noisy channels were replaced by an interpolated weighted average from surrounding electrodes. Data from four participants contained noisy channels, with only a single channel interpolated in each case. A final round of automatic artifact rejection with a threshold of  $\pm 200 \mu\text{v}$  was used to remove any remaining artifacts.

Data analysis focused on three different EEG components – the P1, N170, and P2 components, identified based on previous literature. The P1 was calculated from 110 – 140 ms over electrodes O1 and O2 (Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002). This was used to assess whether the accurate prediction of the emotional content of a face influence early sensory processing (cf. Roussel et al., 2014; Baess et al, 2008). The N170 was measured from 155 – 190 ms electrodes P7 and P8 (Bentin et al., 1996; Eimer, 2000). The P2 component was calculated using the average amplitude from 200 – 300 ms, from electrodes P7 and P8 for the P2 (Eimer and Holmes, 2002; Hughes & Waszak, 2014). Average amplitudes were calculated for each component by taking the mean activity across the defined time windows, averaged across the specified electrodes. Statistical analysis was conducted using repeated measure ANOVA with the factors emotion (fear and neutral) and

congruency (congruent and incongruent). Statistical analysis of the behavioral ratings were also analyzed using a repeated measures ANOVA.

## Results

### *Behavioral Results*

Analysis of the behavioral data focused on participants fear ratings. Repeated measures ANOVA revealed a significant main effect of emotion ( $F(1,22) = 287.3; p < .001$ ), as well as a significant interaction between emotion and congruency ( $F(1,22) = 5.12; p < .05$ ). The main effect of emotion simply reflects the fact that participants rated the fearful faces as containing more fear compared to neutral faces. Paired-sampled  $t$ -tests were used to investigate the significant emotion x congruency interaction. These revealed that congruent fearful faces were rated as significantly more fearful than incongruent fearful faces ( $t(22) = 2.5; p < .05$ ). Meanwhile, there was no significant difference between congruent neutral faces and incongruent neutral faces ( $t(22) = 1.37; p = .19$ ). Overall, these findings show that correct prediction of a fearful face led to a significant increase in the fear perceived in the face. Although no significant effect was observed for neutral faces, the direction of the fear rating points to the possibility that correct prediction of neutrality (i.e. no fear) increased the perception of neutrality. Taken together, these findings suggest that behavioral ratings are *facilitated* by accurate action effect prediction, since predicted fearful faces were rated as significantly more fearful, while predicted neutral faces were rated as somewhat more neutral (less fearful).

### *ERP Results*

Analysis of the P1 revealed no significant main effects and no significant interaction ( $F_s < 1$ ). Analysis of the N170 component (see Figure 2) revealed a significant main effect of emotion ( $F(1,22) = 30.9; p < .001$ ) and a significant emotion x congruency interaction ( $F(1,22) = 8.7; p < .01$ ). The main effect of emotion was characterized by a greater N170 for fearful ( $M = -3.89; SEM = .836$ ) compared to neutral ( $M = -1.62; SEM = 1$ ) faces. Figure 2B shows the topography of this effect, exhibiting a posterior maxima across both parietal and occipital electrodes. Further analysis at occipital leads (averaged between O1 and O2), revealed significant effect of emotion ( $F(1,22) = 26.7; p < .001$ ), confirming this emotion effect to be more widespread than an isolated component over temporal parietal electrodes. A significant emotion x congruency interaction was also observed at these electrodes ( $F(1,22) = 5.36; p < .05$ ).

Next, to further clarify the significant interaction between emotion and congruency, paired-sampled t-tests were conducted at temporal parietal leads as well as occipital electrodes. At P7 and P8 a significant difference was observed between congruent and incongruent conditions for fearful faces ( $t(22) = 2.46; p < .05$ ), but not for neutral faces ( $t(22) = 1.6; p = .14$ ). A similar pattern was observed at occipital sites, with congruent versus incongruent fearful faces approaching significance ( $t(22) = 1.99; p = .059$ ), but no effect for the same comparison for neutral faces ( $t(22) = 1.05; p = .3$ ). These findings highlight that significant attenuation was present for accurately predicted fearful faces over posterior electrode sites, but no such attenuation was observed for neutral faces. These findings suggest that the ERP response over posterior electrodes to a fearful face is significantly attenuated when its emotional content is consistent with participants' action prediction. In contrast, neutral images show no attenuation at lateral parietal or occipital leads (Figure 2D)<sup>1</sup>.

Analysis of the P2 time window at electrodes P7 and P8 revealed a significant main effect of emotion ( $F(1,22) = 8.42; p < .05$ ), and a significant emotion by congruency interaction ( $F(1,22) = 11.23; p < .05$ ). Paired sampled  $t$ -tests revealed a significant difference between congruent and incongruent fearful faces ( $t(22) = 2.3; p < .05$ ), but no difference between congruent and incongruent neutral faces ( $t(22) = 1.54; p = .138$ ). In addition, the effect of emotion, was confined to incongruent stimuli ( $t(22) = 3.63; p < .01$ ) and not congruent stimuli ( $t(22) = 1.13; p = .272$ ). These findings show that the effects of congruency for fearful faces extends beyond the N170 time window, into the later P2 peak.

## Discussion

The present study aimed to investigate behavioral and neurophysiological responses to fearful and neutral faces that were predicted based on a participant's choice of voluntary action. The behavioral data showed that accurate action prediction resulted in an increase of the emotional rating, such that predicted fearful faces were rated as significantly more fearful. The ERP data revealed that predicted fearful faces showed an attenuated fear response over posterior electrodes, while no such attenuation was observed for neutral faces.

The current study included both ERP and behavioral indices of the sensory processing of action effects. While ERP responses were reduced for congruent fearful faces, behavioral ratings were increased. Although somewhat counterintuitive, closer consideration reveals that this fits well with other recent studies. In most previous studies participants were probed on the strength of the processing of congruent and incongruent action effects, either using luminance ratings (Roussel et al., 2013, 2014), or using stimulus detection (Cardoso-Leite et al., 2010). According to the preactivation account of sensory attenuation (Roussel et al., 2013, 2014; Waszak et al., 2012), preparation of a particular action entails activation of the

predicted action effect. Under this account, the reduced magnitude of sensory processing occurs because the stimulus-driven response (i.e. the increase from the elevated pedestal level) is smaller when a stimulus is preactivated. Thus, although the overall signal is amplified for congruent stimuli, the change from pedestal is smaller for preactivated stimuli, meaning reduced sensitivity when detecting the stimulus from noise. Importantly, in the current study participants were asked to rate the content of the action effect stimuli, and not their strength. As such, participants would no longer compare the signal distribution to a noise distribution (with no stimulus) to determine stimulus strength, rather they would compare the two signal distributions (neutral and fear), and since both will be amplified, accurate expression prediction should result in improved stimulus discrimination. Indeed, one recent study, using a coherent motion paradigm observed similar behavioral findings to those reported here, namely that stimulus discrimination is improved by accurate action effect prediction (Desantis, Roussel, & Waszak, 2014).

In contrast to the behavioral data, ERPs for congruent stimuli were attenuated in comparison to incongruent stimuli. So, how might one reconcile behavioral amplification with neurophysiological attenuation? Assuming that action preparation preactivates predicted action effects, reduced neurophysiological processing of congruent stimuli may reflect a form of repetition suppression, whereby repeated stimuli show reduced neural response (for a review see Grill-Spector, Henson, & Martin, 2006). One possible mechanism for repetition suppression is that the reduced neural response reflects more efficient coding of information (Grill-Spector et al., 2006). As such, reduced neural processing could still reflect enhanced stimulus representation (Schacter & Buckner, 1998), as suggested by our behavioural results. Indeed, as well as showing reduced neural responses, repeated stimuli typically also show improved recognition, a phenomenon known as repetition priming (Tulving & Schacter, 1990). As such, the reduced neurophysiological response alongside enhance behavioral

discrimination observed in the present study, highlights the possible common mechanism for sensory attenuation, repetition priming and repetition suppression (Waszak et al., 2012).

The significant attenuation observed in the N170 component is in contrast to one previous study investigating ERP responses to face and house action effect stimuli (Hughes & Waszak, 2014), where attenuation was only observed on the later P2 peak. However, this previous study only used faces with neutral expressions, which also showed no significant N170 attenuation in the present study. Indeed, both behavioral and ERP measures showed more reliable modulations as a function of action prediction in the fearful condition than in the neutral condition. This suggests that emotional stimuli are subject to greater attenuation than non-emotional stimuli.

The current finding may have important implications for the role of emotion in pre-reflexive agency. Although not previously investigated with sensory attenuation, such questions are beginning to be assessed in intentional binding, another phenomenon related to pre-reflexive agency (Moore & Obhi, 2012). Intentional binding refers to the observation that voluntary action effects are perceived as earlier in time, compared to the same stimuli occurring in isolation (Haggard, Clark, & Kalogeras, 2002), and like sensory attenuation, is thought to result from predictive action mechanisms (Waszak et al., 2012). Yoshie and Haggard (2013) showed that intentional binding is reduced for sounds related to fear and disgust, while it is increased for sounds related to achievement and amusement. Takahata et al. (2012), meanwhile, showed greater binding for tones previously associated with monetary gains, compared with tones associated with monetary losses. These authors suggest that increased binding to positive outcomes reflects the self-serving bias; that is the tendency to over attribute positive outcomes to being caused by oneself (Mezulis, Abramson, Hyde, & Hankin, 2004). The present study extends these findings to show that like intentional binding, sensory attenuation is modulated by the valence of the action effects. In contrast to those

previous studies, however, greater attenuation was observed for negative stimuli (fearful faces) compared to neutral stimuli (neutral faces). One possible explanation for this difference is that fearful face stimuli could be interpreted as positive to the observer. A central aspect of social behavior is that physical confrontation can often be avoided through the use of threatening and submissive nonverbal displays. Marsh, Ambady, and Kleck (2005) showed that while angry facial expressions are associated with avoidance-related behaviors, fear is associated with approach related-behaviors. They suggest that fearful expressions may serve as a social cue to facilitate approach towards the expresser due to their submissive and affiliative nature. As such, social context will be crucial in determining whether an outcome is classed as appetitive or aversive. By manipulating both the emotional valence and the social context, future research can provide further insight into the how pre-reflexive measures of agency, such as sensory attenuation and intentional binding might be modulated in social interaction.

It is important to note that no explicit measures of agency were recorded in the present study, and that therefore the observed N170 attenuation might reflect sensory processing unrelated to agency. Indeed, the links between sensory attenuation, intentional binding, and sense of agency remain controversial (Dewey & Knoblich, 2014). A possible alternative explanation for the heightened cortical response to unexpected fearful faces observed in the present study may be related to their potential to signal danger. Previous research has found differential amygdala activation to emotional faces as early as 120ms after stimulus onset (Halgren et al., 1994). Furthermore, patients with damage to amygdala do not show the same increased activity in fusiform and occipital cortex to fearful faces observed in healthy volunteers (Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004). These findings suggest that increased cortical responses to fearful faces are modulated by a fast response to fearful stimuli in the amygdala. In the present study, the unexpected fearful face



might invoke a particularly strong amygdala response, triggering attention towards the face and thus increasing the cortical response to the face. As such, the difference observed between congruent and incongruent fearful faces might reflect an emotion driven modulation of attention, rather than an effect of motor prediction. By incorporating additional measures of implicit and explicit agency, future research should clarify the precise relationship between low-level motor prediction phenomena, and feelings of agency for emotional outcomes.

The present study investigated the social and affective factors that modulate sensory attenuation. Both behavioral and ERP responses to predicted action effects showed greater modulation to fearful faces than neutral faces. Since previous research in this domain has largely focused on simplistic sensory stimuli, of little social significance, this provides novel insight into how motor prediction shapes our understanding of our social world.

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## References

- Baess, P., Jacobsen, T., & Schroger, E. (2008). Suppression of the auditory N1 event-related potential component with unpredictable self-initiated tones: evidence for internal forward models with dynamic stimulation. *Int J Psychophysiol*, *70*(2), 137-143. doi: 10.1016/j.ijpsycho.2008.06.005
- Batty, M., & Taylor, M. J. (2003). Early processing of the six basic facial emotional expressions. *Brain Res Cogn Brain Res*, *17*(3), 613-620. doi: 10.1016/S0926-6410(03)00174-5
- Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological Studies of Face Perception in Humans. *J Cogn Neurosci*, *8*(6), 551-565. doi: 10.1162/jocn.1996.8.6.551
- Blakemore, S. J., Frith, C. D., & Wolpert, D. M. (1999). Spatio-temporal prediction modulates the perception of self-produced stimuli. *J Cogn Neurosci*, *11*(5), 551-559.
- Blakemore, S. J., Wolpert, D., & Frith, C. (2000). Why can't you tickle yourself? *Neuroreport*, *11*(11), R11-16.
- Blau, V. C., Maurer, U., Tottenham, N., & McCandliss, B. D. (2007). The face-specific N170 component is modulated by emotional facial expression. *Behav Brain Funct*, *3*, 7. doi: 10.1186/1744-9081-3-7
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*(4), 433-436. doi: Doi 10.1163/156856897x00357
- Cardoso-Leite, P., Mamassian, P., Schutz-Bosbach, S., & Waszak, F. (2010). A new look at sensory attenuation: action-effect anticipation affects sensitivity, not response bias. *Psychol Sci*, *21*(12), 1740-1745.
- Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J Neurosci Methods*, *134*(1), 9-21.
- Desantis, A., Roussel, C., & Waszak, F. (2014). The temporal dynamics of the perceptual consequences of action-effect prediction. *Cognition*, *132*(3), 243-250. doi: 10.1016/j.cognition.2014.04.010
- Dewey, J. A., & Knoblich, G. (2014). Do Implicit and Explicit Measures of the Sense of Agency Measure the Same Thing? *PLoS One*, *9*(10). doi: 10.1371/journal.pone.0110118
- Di Russo, F., Martinez, A., Sereno, M. I., Pitzalis, S., & Hillyard, S. A. (2002). Cortical sources of the early components of the visual evoked potential. *Hum Brain Mapp*, *15*(2), 95-111.
- Eimer, M. (2000). The face-specific N170 component reflects late stages in the structural encoding of faces. *Neuroreport*, *11*(10), 2319-2324.
- Eimer, M., & Holmes, A. (2002). An ERP study on the time course of emotional face processing. *Neuroreport*, *13*(4), 427-431.
- Ekman, P., & Friesen, W. V. (1976). *Pictures of Facial Affect*. Palo Alto, CA: Consulting Psychologists Press.
- Frith, C. D. (2012). Explaining delusions of control: the comparator model 20 years on. *Conscious Cogn*, *21*(1), 52-54. doi: 10.1016/j.concog.2011.06.010
- Frith, C. D., Blakemore, S. J., & Wolpert, D. M. (2000). Abnormalities in the awareness and control of action. *Philos Trans R Soc Lond B Biol Sci*, *355*(1404), 1771-1788.

- Gosling, A., & Eimer, M. (2011). An event-related brain potential study of explicit face recognition. *Neuropsychologia*, 49(9), 2736-2745. doi: 10.1016/j.neuropsychologia.2011.05.025
- Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: neural models of stimulus-specific effects. *Trends Cogn Sci*, 10(1), 14-23. doi: 10.1016/j.tics.2005.11.006
- Haggard, P., Clark, S., & Kalogeras, J. (2002). Voluntary action and conscious awareness. *Nat Neurosci*, 5(4), 382-385.
- Halgren, E., Baudena, P., Heit, G., Clarke, J. M., Marinkovic, K., & Clarke, M. (1994). Spatio-temporal stages in face and word processing. I. Depth-recorded potentials in the human occipital, temporal and parietal lobes. *J Physiol Paris*, 88(1), 1-50.
- Hughes, G., Desantis, A., & Waszak, F. (2013a). Attenuation of auditory N1 results from identity-specific action-effect prediction. *Eur J Neurosci*, 37(7), 1152-1158. doi: 10.1111/ejn.12120
- Hughes, G., Desantis, A., & Waszak, F. (2013b). Mechanisms of intentional binding and sensory attenuation: the role of temporal prediction, temporal control, identity prediction, and motor prediction. *Psychol Bull*, 139(1), 133-151. doi: 10.1037/a0028566
- Hughes, G., & Waszak, F. (2011). ERP correlates of action effect prediction and visual sensory attenuation in voluntary action. *Neuroimage*, 56(3), 1632-1640. doi: 10.1016/j.neuroimage.2011.02.057
- Hughes, G., & Waszak, F. (2014). Predicting faces and houses: Category-specific visual action-effect prediction modulates late stages of sensory processing. *Neuropsychologia*, 61C, 11-18. doi: 10.1016/j.neuropsychologia.2014.06.002
- Marsh, A. A., Ambady, N., & Kleck, R. E. (2005). The effects of fear and anger facial expressions on approach- and avoidance-related behaviors. *Emotion*, 5(1), 119-124. doi: 10.1037/1528-3542.5.1.119
- Mezulis, A. H., Abramson, L. Y., Hyde, J. S., & Hankin, B. L. (2004). Is there a universal positivity bias in attributions? A meta-analytic review of individual, developmental, and cultural differences in the self-serving attributional bias. *Psychol Bull*, 130(5), 711-747. doi: 10.1037/0033-2909.130.5.711
- Moore, J. W., & Obhi, S. S. (2012). Intentional binding and the sense of agency: a review. *Conscious Cogn*, 21(1), 546-561. doi: 10.1016/j.concog.2011.12.002
- Roussel, C., Hughes, G., & Waszak, F. (2013). A preactivation account of sensory attenuation. *Neuropsychologia*. doi: 10.1016/j.neuropsychologia.2013.02.005
- Roussel, C., Hughes, G., & Waszak, F. (2014). Action prediction modulates both neurophysiological and psychophysical indices of visual sensory attenuation. *Front Hum Neurosci*, 8(115).
- Sato, A. (2008). Action observation modulates auditory perception of the consequence of others' actions. *Conscious Cogn*, 17(4), 1219-1227.
- Schacter, D. L., & Buckner, R. L. (1998). Priming and the brain. *Neuron*, 20(2), 185-195.
- Stenner, M. P., Bauer, M., Sidarus, N., Heinze, H. J., Haggard, P., & Dolan, R. J. (2014). Subliminal action priming modulates the perceived intensity of sensory action consequences. *Cognition*, 130(2), 227-235. doi: 10.1016/j.cognition.2013.11.008
- Takahata, K., Takahashi, H., Maeda, T., Umeda, S., Suhara, T., Mimura, M., & Kato, M. (2012). It's not my fault: postdictive modulation of intentional binding by

- monetary gains and losses. *PLoS One*, 7(12), e53421. doi: 10.1371/journal.pone.0053421
- Vuilleumier, P., Richardson, M. P., Armony, J. L., Driver, J., & Dolan, R. J. (2004). Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nat Neurosci*, 7(11), 1271-1278. doi: 10.1038/nn1341
- Waszak, F., Cardoso-Leite, P., & Hughes, G. (2012). Action effect anticipation: neurophysiological basis and functional consequences. *Neurosci Biobehav Rev*, 36(2), 943-959. doi: 10.1016/j.neubiorev.2011.11.004
- Yoshie, M., & Haggard, P. (2013). Negative Emotional Outcomes Attenuate Sense of Agency over Voluntary Actions. *Curr Biol*, 23(20), 2028-2032. doi: 10.1016/j.cub.2013.08.034

### Figure Captions

Figure 1: Timeline of the experimental procedure.

Figure 2: ERPs at electrodes P7 and P8 (a). Topographic plots for (b) fearful minus neutral faces, (c) incongruent fearful faces minus congruent fearful faces, and (d) incongruent neutral faces minus congruent neutral faces.

### Footnotes

1. Inspection of the topography (Figure 2D) of the difference between congruent and incongruent neutral faces showed a somewhat less posterior distribution than that observed for the main effect of emotion, or the effect of congruency in fear trials. Thus, further analysis was conducted at electrode Pz to investigate whether these differences were significant. This revealed a significant interaction between emotion and congruency ( $F(1,22) = 22.2; p < .05$ ). Subsequent t-tests revealed a near significant difference between congruent and incongruent trials for neutral faces ( $t(22) = 1.96; p = .063$ ), but not for fearful faces ( $t(22) = 1.34; p = .194$ ).

## Tables

Table 1: Mean (and standard error) behavioral ratings.

	<i>Congruent</i>	<i>Incongruent</i>
<i>Fear</i>	80.2 (2.78)	78.9 (2.76)
<i>Neutral</i>	11.9 (1.78)	12.5 (1.82)

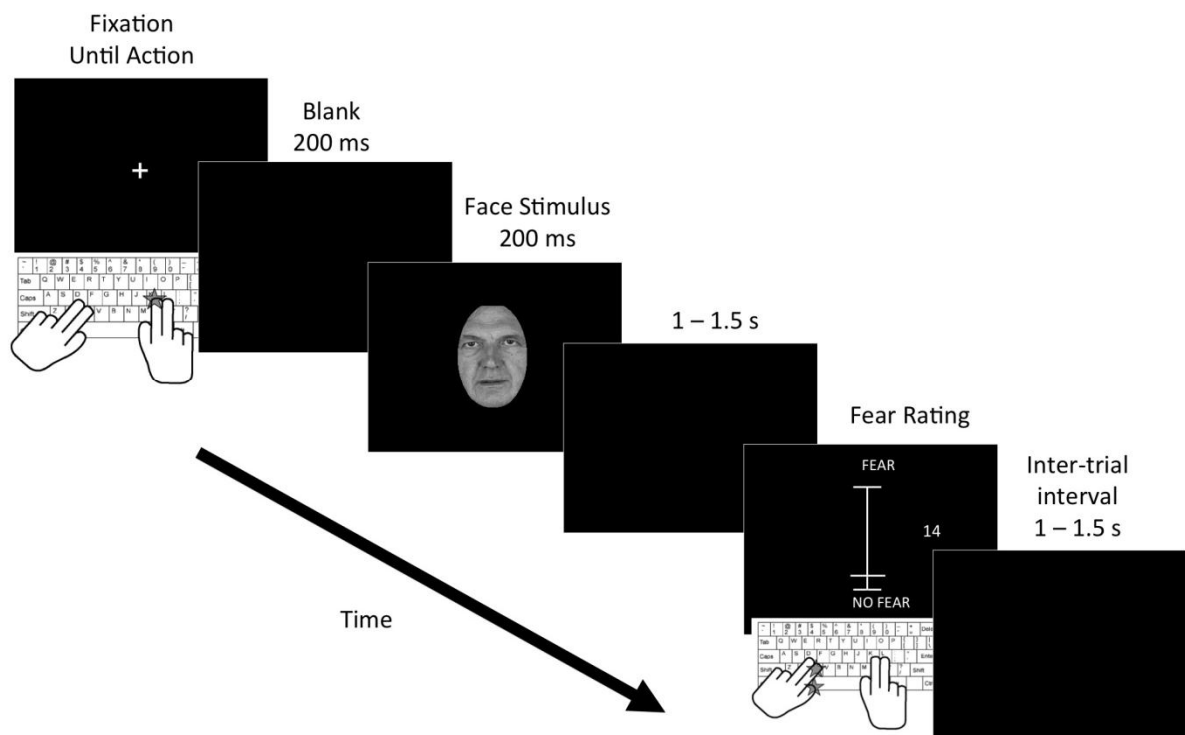


Fig. 1

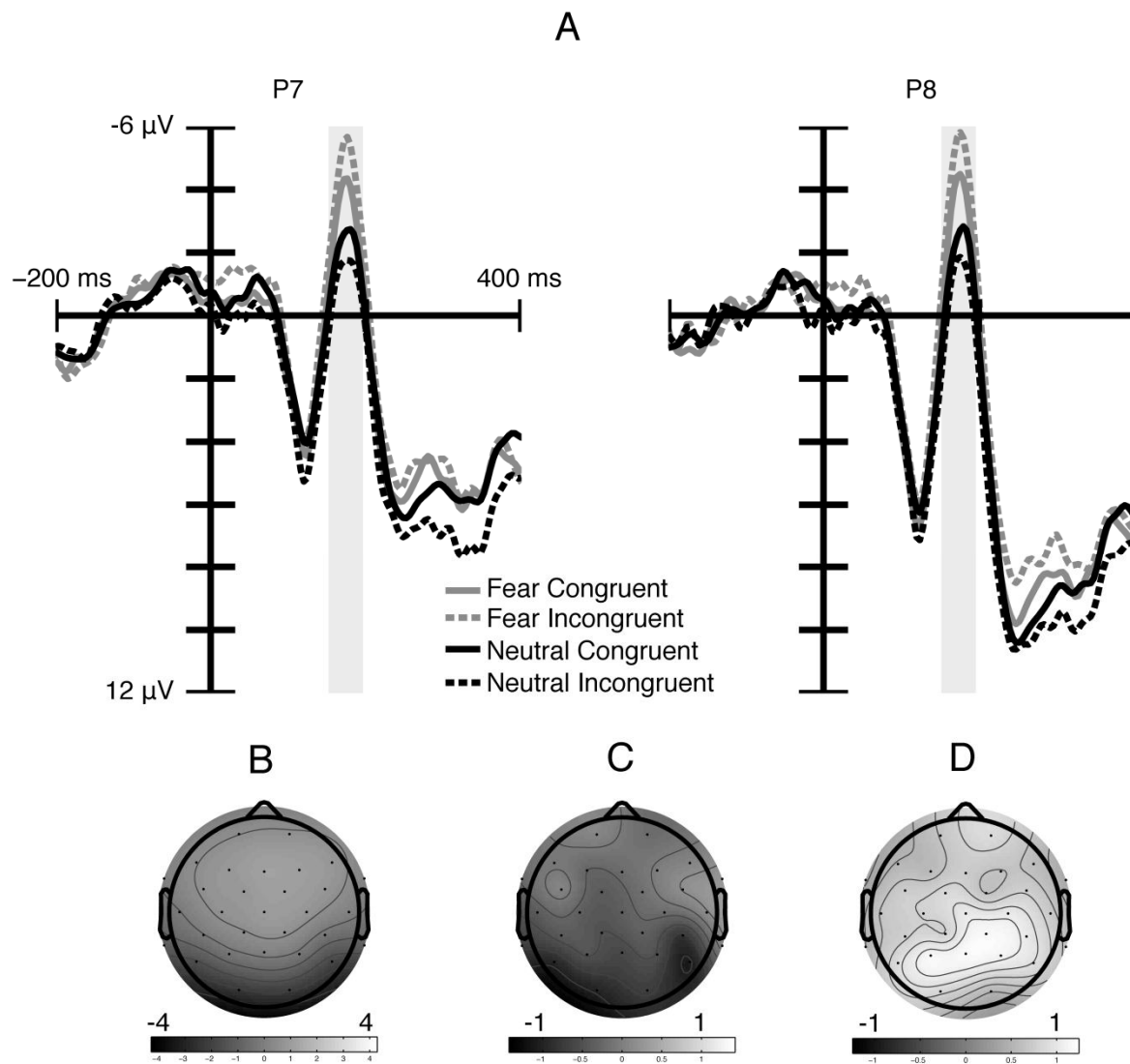


Fig. 2