

SENSORY ATTENUATION OF ACTION EFFECTS DUE TO PREDICTIVE FORWARD
MODELS: WHEN DOES IT TRANSFER TO OBSERVED ACTIONS?

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A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Psychology

2012

ABSTRACT

SENSORY ATTENUATION OF ACTION EFFECTS DUE TO PREDICTIVE FORWARD MODELS: WHEN DOES IT TRANSFER TO OBSERVED ACTIONS?

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The sensory consequences of intentional actions (action effects) are often judged to be less intense compared to identical but externally generated stimuli. This phenomenon is normally explained in terms of predictive forward models within the sensorimotor system which partially inhibit predictable sensory feedback. An unsettled question is whether merely observing another agent performing a predictable action may also trigger a forward model with attendant sensory attenuation, or alternatively, if a self-generated motor signal is necessary. I conducted three experiments to investigate this question using a visual speed discrimination task. Participants judged which of two moving stimuli was faster. The first stimulus was initiated by the participant's own key press (Self), another person's key press (Other), or the computer program (Computer), and had a fixed speed. The second stimulus was always initiated by the computer and had a variable speed. The point of subjective equality (PSE) was compared for each condition. In Experiment 1 participants performed the task at their own pace. The Self condition was judged to be slower than the Other or Computer conditions, while the latter two did not differ. To control for the possibility that self-initiated movements were more temporally predictable and/or less attended than movements by other agents, in Experiment 2 the pace was controlled by go signals, and a green light followed every human or computer action to indicate that a movement was about to begin. Compared to Experiment 1, the PSE increased in all conditions, but the Self condition was still

judged to be slowest and the Computer condition the fastest, while the Other condition was in between. In Experiment 3 the predictability of the action effects was manipulated independently from the agent who produced them, in order to investigate whether expectation similarly attenuates the intensity of Self and Computer-initiated action effects. Participants used two keys to initiate moves in two directions (left or right). In the Predictable group, the direction of the move matched the direction of the key press 80% of the time. In the Unpredictable group, the directions only matched 50% of the time. Self moves were only attenuated in the Predictable group. I conclude that sensory attenuation is influenced by a combination of private and shared or publicly available information, and that the influence of public information may be particularly tuned to biological agents. Furthermore action effects must be predictable to become attenuated.

ACKNOWLEDGMENTS

I would like to thank my faculty mentor Thomas Carr, and committee members Timothy Pleskac, Taosheng Liu, and Susan Ravizza for their helpful comments. Special thanks also go to current and former research assistants Mura Dominko, Hillary Hicks, Lucas Petto, Zack Hardin, and Claire Grazal, for invaluable help with data collection, and to Denise Carr for bringing cookies.

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INTRODUCTION

The predictable sensory consequences of voluntary actions, henceforth “action effects”, are often judged to be less intense, or attenuated, compared to identical but externally generated stimuli. This finding has been reproduced across several sensory domains: self-initiated action effects (e.g. stimuli triggered by a button press or other voluntary movement) are judged to be less loud (Sato, 2008; Weiss, Herwig, & Schütz-Bosbach, 2011a; Weiss, Herwig, & Schütz-Bosbach, 2011b), less forceful (Shergil, Bays, Frith, & Wolpert, 2003; Bays, Wolpert, & Flanagan, 2005), and less ticklish (Blakemore, Wolpert, & Frith, 1998) than equivalent stimuli generated by a computer or machine apparatus.

Similar differences between self-initiated and externally presented stimuli have been reported at the neural level. For example, self-initiated sounds have been associated with a lower blood oxygen level dependent (BOLD) response in auditory cortex compared to external sounds (Martikainen, Kaneko, & Hari, 2005). Self- and externally initiated action effects have also been compared by means of ERPs. The N1 is a negative deflection around 100-150 ms post stimulus thought to be associated with early cortical processing of sensory stimuli. Predictable and self-initiated action effects evoke lower amplitude N1 responses compared to identical but externally triggered effects. For example, Baess, Widmann, Roye, Schroger, and Jacobsen (2009) found a reduced auditory N1 for self-initiated tones compared to externally triggered tones, and Hughes and Waszak (2011) found attenuated cortical responses over frontal and parietal areas to self-initiated visual effects starting around 150 ms post stimulus. These

results suggest cortical sensory attenuation occurs at an early stage in perception, with the caveat is that no study has simultaneously assessed phenomenological and neurophysiological indices of attenuation.

Attenuated sensory responses, whether neurophysiological or phenomenological, are normally explained in terms of predictive forward models (Waszak, Cardoso-Leite, & Hughes, 2011). Forward models are postulated neural processes that simulate responses within the motor system to estimate upcoming action effects (Wolpert, Ghahramani, & Johnson, 1995). In its simplest form, a forward model takes the input of a motor command and outputs a predicted action effect. More realistic and complex models incorporating sensory feedback can make predictions for upcoming action effects based on a broader array of information about the current environment, as well as past experience (Powers, 1978; Körding & Wolpert, 2004).

Forward models are considered to be involved in various functions including motor guidance and awareness of an individual's own actions. For example, efferent motor information has been found to play a role differentiating the effects of one's own actions from effects caused by the external environment (Tsakiris, Haggard, Franck, Mainy, & Sigiru, 2005). In another study, participants were more likely to misattribute self-initiated tones triggered by their own button presses to another agent when the tones deviated from the expected frequency or followed the button press at a longer than expected delay (Sato & Yasuda, 2005). Regarding sensory attenuation, the general explanation is that a predictive forward model partially cancels the predictable components of action effects. However, some details of the scope of this phenomenon and its mechanisms remain unclear.

In a set of experiments investigating ticklishness, Blakemore et al. (1998) had participants tickle their own right palms using a robotic arm controlled by their left arm. Introducing spatial and temporal perturbations between the input and output increased perceived ticklishness of the self-stimulation, suggesting a relationship where more accurate prediction of sensory consequences leads to attenuation of (tactile) action effects. The authors argued more specifically that a corollary discharge or “efference copy” of outgoing motor signals selectively attenuated the tactile sensations expected to result from performing those movements (as described in Wolpert, Ghahramani, & Jordan, 1995; Wolpert 1997). By this account sensory attenuation should only be observed for action effects produced by voluntary movements. More recently, however, a study by Voss, Ingram, et al. (2006) used TMS to delay the output of voluntary movements, and found attenuation of tactile sensation during the delay. This suggests that sensory attenuation may rely on signals related to the preparation for movement, rather than actually executing movements.

An ongoing debate related to sensory attenuation is whether it is a special property unique to self-initiated actions, or alternatively, reflects a general prediction mechanism that might be applied to other types of perceptual events (e.g. Blakemore, Rees, & Frith, 1998; Lange, 2011). An idea which has gained popularity in recent decades is that actors may be able to predict the consequences of others' actions by simulating the action within their own motor system. This is supported by studies on monkeys and humans which show that observing an action, even when the observer has no intention to act, activates many of the same neural substrates in motor and pre-motor cortex as performing the action (e.g. Buccino, Fink, et al., 2000; Hari, Forss, et

al., 1998; Schütz-Bosbach & Prinz, 2007). The extent of frontal and motor activation depends on the degree of overlap between the action repertoire of the actor and observer (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005). Similarly, processing action-related language also activates regions of pre-motor cortex, dependent on the level of specialized motor experience (Beilock, Lyons, Mattarella-Micke, Nusbaum, & Small, 2008). These types of findings have led to proposals that motor system allows observers to understand the actions of others by mapping observed actions onto their own action representations without executing them (Rizzolatti & Craighero, 2004). Much the same idea has been suggested in the literature on speech perception and language acquisition (Galantucci, Fowler, & Turvey, 2006).

Along similar lines, there has been recent interest in whether a predictive forward model with attendant sensory attenuation could be activated by merely observing another agent's action (Sato, 2008; Weiss et al., 2011a, 2011b). By testing if and when action effects initiated by other actors are attenuated in a similar fashion to self-initiated actions, some inferences can be drawn about how humans predict the consequences of actions via forward models. One possibility is that sensory attenuation is a unique property of intentional action. I will refer to this as the *self attenuation hypothesis*. For example, sensory attenuation might depend specifically on private motor or pre-motor information, e.g. an efference copy of the motor signal, or the intention to initiate a motor action. Weiss and colleagues have argued that “one’s own agentive influence on the outside world has a special perceptual quality which distinguishes it from any external influence” (Weiss et al., 2011a).

Another possibility is that sensory attenuation depends primarily on the objective predictability of action effects, rather than being specifically tied to activity in the motor system. I will refer to this as the *prediction based hypothesis*. According to this view, self-initiated action effects are normally attenuated because they also tend to be more predictable than other perceptual events, both with respect to their form and their timing. This hypothesis predicts that a more predictable action effect should be attenuated compared to a less predictable action effect, regardless of who caused it.

A third possibility is that sensory attenuation is not unique to self-initiated action effects, but does depend on inferring some human-like agency or intent on the part of the actor. I will refer to this as the *biological attenuation hypothesis*. Humans are highly social creatures, and rely heavily on the ability to perceive what others are doing as well as inferring intentions from gesture. The human visual system is also very sensitive to motion kinematics characteristic of humans and other animals (see Blake & Shiffrar, 2007 for a review). Therefore it seems plausible that forward models in humans could be specialized for predicting actions performed by biological agents. This view receives some support from the literature on a phenomenon known as intentional binding. When individuals perform intentional actions, there is a perceived compression of the time between the action and the sensory consequences (e.g. Haggard, Clark, & Kalogeras, 2002). Interestingly, intentional binding has been observed for both self- and other-initiated action effects, but not for those triggered by machines (Wohlschläger, Haggard, Gesierich, & Prinz, 2003). This seems consistent with the biological attenuation hypothesis, although the relationship between intentional binding and sensory attenuation is unknown. The biological attenuation hypothesis predicts that action

effects initiated by oneself or another human actor should be attenuated compared to equivalent stimuli produced by a computer, even if the objective predictability of each condition is the same.

Evidence for (and against) attenuation of observed action effects

To my knowledge, only three previous studies have compared the perceived intensity of action effects initiated by the self, another person, or a non-biological agent, while also attempting to balance the predictability of self- and the externally-initiated action effects. The first, by Sato (2008), supports the biological attenuation hypothesis. The second, by Weiss, Herwig, and Schütz-Bosbach (2011a), supports the self attenuation hypothesis. The third, also by Weiss, Herwig, and Schütz-Bosbach (2011b), supplies part of the foundation for the prediction based hypothesis.

Sato (2008) introduced a general method for studying sensory attenuation. Participants compared the subjective loudness of tones that were either initiated by the participant pressing a button (Self), the experimenter pressing the same button (Other), a machine arm pressing a key (Machine), or simply played through computer speakers (Listen). In all conditions, a standard tone (always 74 dB) was followed by a comparison tone (71, 72, 73, 74, 75, 76, or 77 dB), which participants had to judge as either louder or quieter than the standard tone. The point of subjective equality (PSE) was computed for each condition. Standard tones initiated by the participant or the other human actor, but not the computer or a machine arm, were attenuated relative to comparison tones (see Figure 1), i.e. the PSE for the comparison tone was significantly less than its objective loudness of 74 dB. This suggested that predictive forward models are

activated by human actions, but not by computer or machine actions, consistent with the biological attenuation hypothesis. Because predictive forward models are also believed to contribute to a sense of agency for action effects (Haggard & Chambon, 2012), participants were also asked to rate to what degree they felt they had produced the first tone on a scale from “not at all” (score = 0) to “very much” (score = 8), in order to see whether the explicit and implicit measures would show a similar pattern. Not surprisingly, agency scores were much higher for the self-initiated tones ($M = 7.29$) than for the tones initiated by the other person ($M = 1.71$), despite the similarity in attenuation. This suggests explicit judgments of agency rely on different (or additional) mechanisms to those on which sensory attenuation relies.

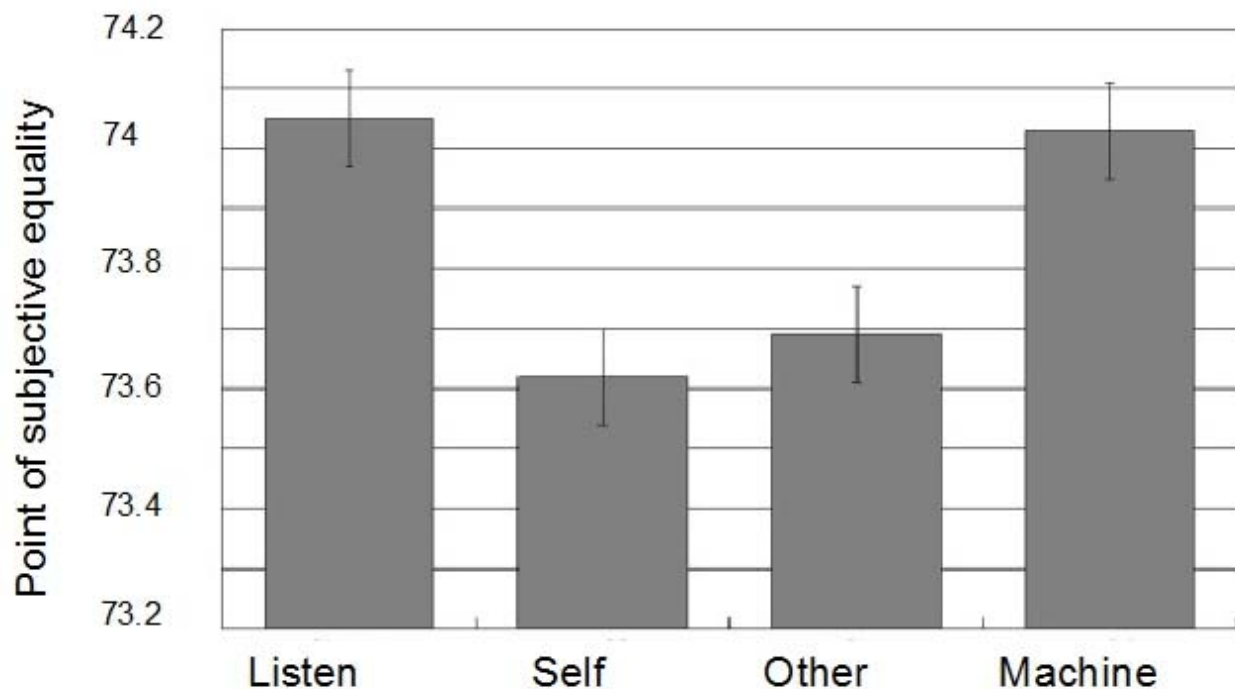


Figure 1. Means and standard errors for the point of subjective equality in each condition of Sato (2008), Experiment 2.

While the results of Sato (2008) support the biological attenuation hypothesis, a second study cast doubt on this result. Using a similar loudness judging paradigm, Weiss, Herwig, and Schütz-Bosbach (2011a) reported that self-initiated tones were attenuated compared to computer-initiated tones, but they did not find any difference between the computer tones and tones produced by another person (see Figure 2). These results are consistent with the self attenuation hypothesis. In contrast to Sato (2008), Weiss et al. (2011a) argue that being an agent (i.e. the initiator of the action-effect) influences the perceptual quality of those action-effects in a way that distinguishes them from all external influences, human as well as non-human.

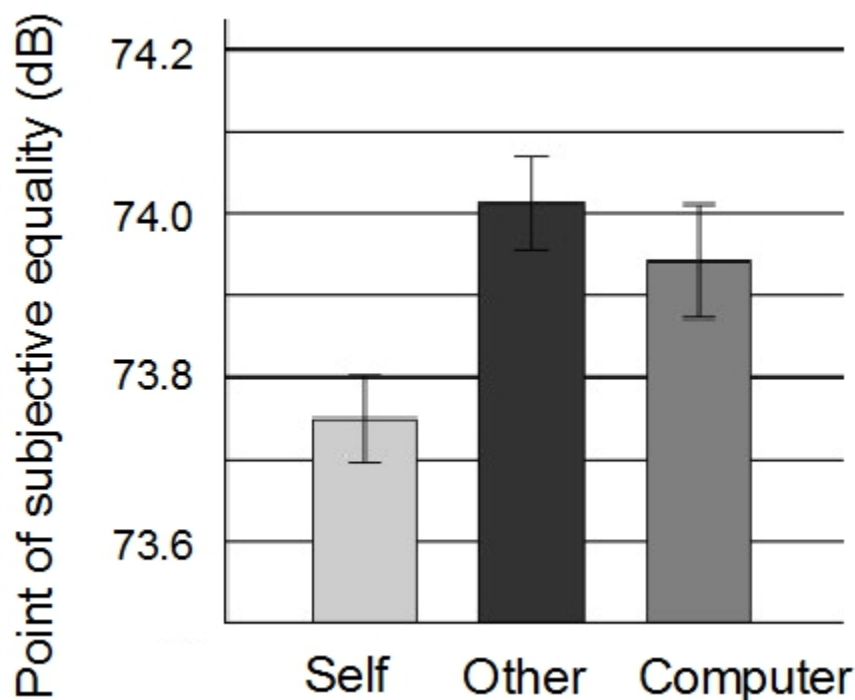


Figure 2. Means and standard errors for the point of subjective equality in each condition of Weiss, Herwig, et al. (2011a), Experiment 2.

Another study, also by Weiss, Herwig, and Schütz-Bosbach (2011b), employed the same general experimental paradigm as the previous two. The novel aspect of this study was the introduction of an Interactive condition where the currently passive agent

“requested” the other person's action by tapping on their arm. This manipulation increased the degree of attenuation in both the Self and Other conditions (see Figure 3) (there was no computer condition in this experiment). The authors suggested the Interactive condition led participants to integrate the other person into their own action representation. Notably, in this study both the Self and Other conditions showed attenuation with respect to the objective 74 dB loudness of the standard tone, although the attenuation was somewhat greater for Self tones. This result is consistent with the biological attenuation hypotheses (passively observed action effects can be attenuated), but also suggests that being an agent influences perception of action effects in a special way.

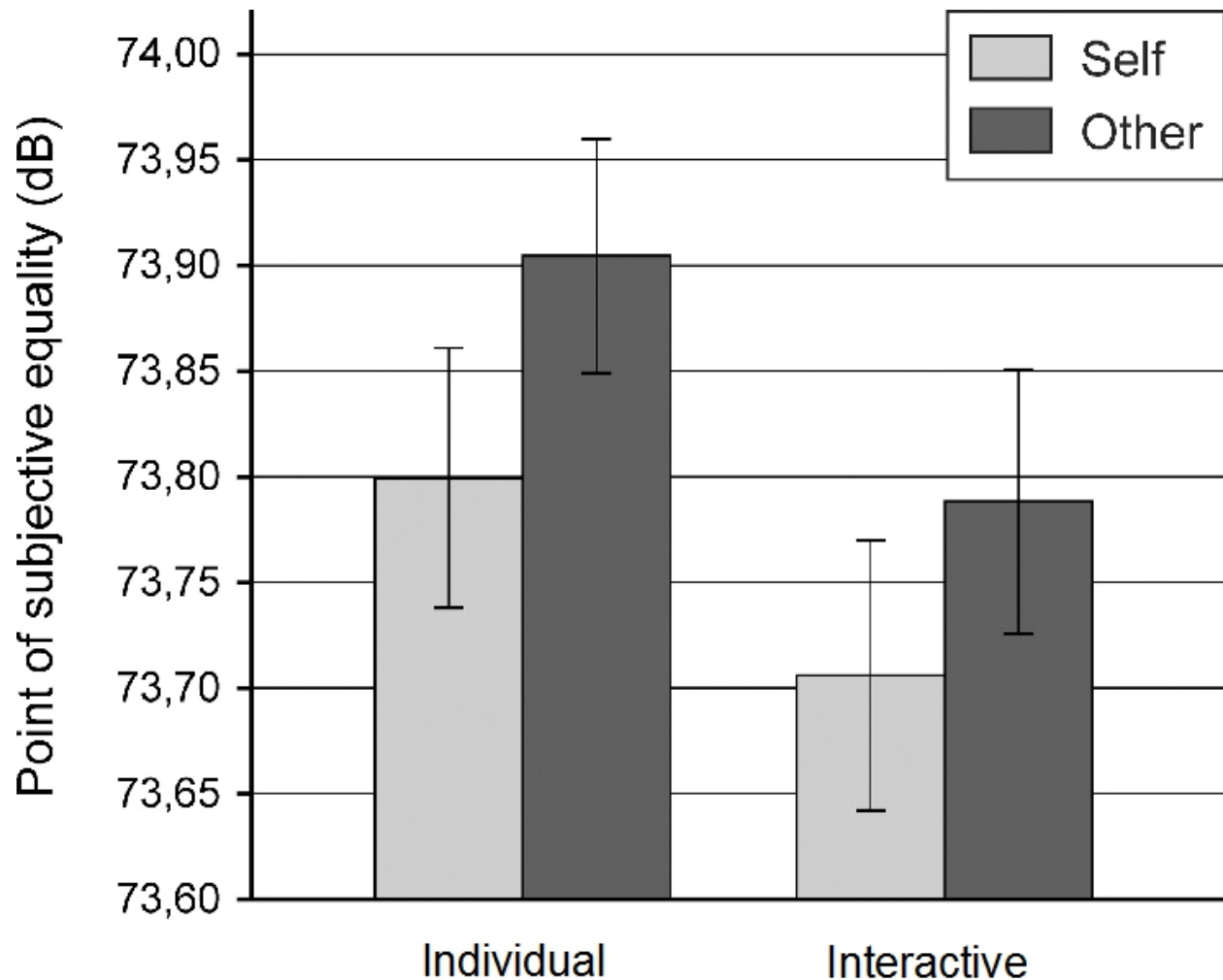


Figure 3. Mean and standard error of the four conditions in Weiss, Herwig et al. (2011b).

To summarize, the three studies described consistently found that self-initiated tones were attenuated compared to tones produced by a machine or computer, and found mixed evidence that tones observed to be initiated by another person may be attenuated in a similar fashion to self-initiated tones.

The inconsistent attenuation of the Other condition across the Sato (2008) and Weiss et al. (2011a) studies may have been due to minor methodological differences. In the former, each of the two human actors used the same button to produce the tones using the same pair of gloves, whereas in the latter each human actor used a different button and the actors did not wear gloves. Another difference is that in Sato (2008), all

the tones during the acquisition phase (where participants learned the action effect relation) were self-initiated, whereas Weiss et al. (2011a) included blocks of self- and other-initiated tones during the acquisition phase. Finally, the two studies were also conducted on populations from two very different cultures (Japan and Germany).

Partly because of these multiple differences, it is difficult to explain why the other person's action effects might be attenuated sometimes but not always. A possible answer, which would be in line with the prediction based hypothesis, is that attenuation of another person's action effect is strongly dependent on its predictability, which includes anticipating the onset time. For example, perhaps the apparatus used in Sato (2008) made the onset of tones in the self and other conditions more comparable than the apparatus used by Weiss et al. (2011a) due to greater visual similarity between conditions. The issue of balancing predictability across conditions is described in further detail in the next section.

Could temporal predictability of action effects and attention account for self-attenuation?

Predictive forward models are thought to specify both the form and the *timing* of action effects (Bayes, Wolpert, & Flanagan, 2005). In order to avoid confounding effects of self-agency or biological agency with temporal predictability, past studies which compared sensory attenuation of action effects initiated by the self, another human, or a non-biological agent attempted to make all three conditions equally predictable. To this end, Sato (2008) and Weiss et al. (2011a,b) requested the human actors to perform their motor actions at self-paced but consistent tempo, and used a fixed tempo for the

presentation of the computer generated stimuli. However, minor differences between the conditions may still have influenced the temporal predictability of the action effects.

In Weiss et al. (2011a), the human actors in the Self and Other conditions performed self-paced button presses which produced a tone following a delay of 50 ms, whereas in the Computer condition a visual warning signal was presented for 500 ms, followed by a 100 ms blank interval, followed by a tone. In other words, the delay between the onset of the visual stimulus for the triggering action (the first movement of a finger, or the computer warning signal) and the resulting tone was slightly over 50 ms for the human actors, but 600 ms for the computer-initiated tones. One might also argue that the first warning occurred earlier for self-initiated tones than for tones initiated by the other human actor, assuming actors were aware of their own intention to move prior to actually moving (although the question of when precisely actors become aware of their intention to act is controversial, e.g. see Libet, Gleason, Wright, & Pearl, 1983; Isham, Banks, Ekstrom, & Stern, 2011). It is unclear whether addressing these timing differences would change Weiss et al's (2011a) results or conclusions. However, it is known that ERP correlates of early auditory events (the N1) are attenuated by expectations for time and pitch (Lange, 2009). Therefore, it seems preferable to use the identical timing for all three conditions.

Another problem with previous studies is that the publicly available visual information for predicting the action effect was not equivalent in all conditions. If visual information contributes to the predictions of forward models, this raises the question of whether the visual information across conditions was equally informative. In both Sato (2008) and Weiss et al (2011a,b), participants looked at their own hands or the

experimenter's hands during the Self and Other conditions respectively, but the visual input during the listen/computer conditions was quite different. In the Listen condition of Sato (2008), participants were instructed to keep their eyes on the button in front of them while they listened to the tones, and in Weiss et al. (2011a) the Computer condition used a visual warning signal that was not presented during the Self and Other conditions.

Differences in temporal predictability and/or the visual warnings presented prior to the action effect in the Self, Other, and Computer conditions might also influence the degree to which the action effect captures attention. A detailed account of the relationship between expectation and attention is well beyond the scope of this paper. Broadly speaking, however, attention selects relevant sensory information for prioritized processing, while expectations (e.g. sensory predictions generated by forward models) help guide attention and constrain interpretations of incoming stimuli based on their prior likelihood (Summerfield & Egnér, 2009). A study by Lamy (2005) provides an example of how temporal predictability can influence attention. In this study, participants' ability to ignore the onset of a salient distracter during a color singleton detection task was improved when the distracters appeared at predictable intervals compared to unpredictable intervals. This suggests more temporally predictable stimuli are less likely to capture attention in an involuntary, bottom-up fashion. Similarly, if self-initiated action effects are more temporally predictable than externally generated action effects, they might also be less attended.

What implications would different levels of attention across conditions have for measuring sensory attenuation? Whereas sensory attenuation is a reduction of

perceived intensity for predictable action effects, attention usually has the opposite effect of boosting or prioritizing the attended stimulus. For example, in the Posner cueing task, participants must discriminate and respond to some feature of a target stimulus (e.g. press a button when a target letter is shown). A classic finding from this paradigm is that presenting a cue in the same location as the upcoming target stimulus (a congruent cue) reduces response times to the target, compared to incongruent cues or trials with no cue (Posner, Snyder, & Davidson, 1980). Although the cues might be said to elicit an “expectation”, decreased response times to the target are normally attributed to increased attention to the target, rather than increased predictability per se.

Another example bears more directly on the relationship between attention and perceived intensity of stimuli. Carrasco, Ling, and Reed (2004) studied whether covert attention influenced perceived contrast of gratings presented in the left or right visual field. Transient cues presented on the side of the upcoming target about 50 ms prior to its occurrence increased apparent contrast, spatial frequency, and gap sizes compared to control conditions with cues at center. Turatto, Vescovi, and Valsecchi (2007) used a similar task to demonstrate that attention increased the perceived speed of moving gratings. These examples suggest that, in contrast to the predictions in forward models, increasing attention to a target may increase the perceived intensity of certain features, such as contrast and speed. Attention can also modulate the N1 ERP component. For example, involuntary switching of attention away from a visual task attenuates the N1 elicited by a visual target stimulus (Alho, Escera, Diaz, Yago, & Serra, 1997).

Accepting that expectation and attention interact to shape perception, it is an open question whether differences in sensory attenuation between Self, Other, and

Computer would remain if minor differences in temporal predictability and/or attention to action effects could be accounted for. For example, in the Sato (2008) and Weiss et al. (2011a) studies, only the computer-initiated tones were preceded by a visual warning signal. Could this have resulted in greater attention to the tones in the computer condition? If so, this might work against detecting any attenuation of computer-initiated tones due to their predictability. Similarly, perhaps the self-initiated tones were the most attenuated in previous studies was because their onset was more predictable and less attention-capturing than the other conditions. Indeed, this might explain the increased sensory attenuation for the Interactive condition of Weiss et al. (2011b). Tapping the other human actor's shoulder to initiate their action may have improved participants' ability to anticipate the onset of the tone, compared to when the other human actor performed the actions at their own pace.

Purpose

There were three main aims of the present study. First, it has been suggested that sensory attenuation is a general property of self-initiated action effects, as opposed to being specific to processes associated with a particular sensory modality (Engbert, Wohlschläger, & Haggard, 2008). This claim has been made on the basis of similar attenuation of ERP responses to unexpected action effects in the somatosensory, auditory and visual domains (see Waszak et al. 2012 for a review). However, direct comparisons of attenuation of self- and other-initiated action-effects have been performed in only two modalities – tactile and auditory – and all the evidence relevant to the three hypotheses under examination comes from studies of audition. The purpose of

Experiment 1 was to confirm the phenomenon of sensory attenuation in the visual modality, using a speed-discrimination task.

In everyday life, visual motion often contributes to the perception that one event has ended or another has begun, and the neural substrates of motion perception have been extensively studied. For example, activity in the MT complex, which is known to be specialized for processing motion, increases with increases in objects' speed (Zacks, Swallow, Vettel, & McAvoy, 2006). However, using a moving visual stimulus raises the issue of what would constitute "attenuation" of the action effect. Intuitively, more energy or force is required to move objects with greater speed, which suggests that an attenuated moving stimulus should be perceived as slower. While attenuation of the speed of moving stimuli has not previously been reported, there is support for the idea that attention influences perceived speed. As was mentioned previously, Turatto et al. (2007) reported that cues which validly oriented spatial attention 50 ms prior to a moving grating increasing the perceived speed of those gratings. Attention is also known to boost perceived contrast, and when gratings moving at the same speed are presented simultaneously, the lower-contrast grating appears slower (Stone & Thompson, 1992). Whereas attention prioritizes processing of stimuli, expectancy reduces the likelihood of attentional capture (Lamy, 2005). Therefore, I predicted that an attenuated visual movement would appear to move more slowly, opposite the effects of increased attention.

Assuming that sensory attenuation occurs in the visual modality, a second aim was to compare the self-attenuation, biological attenuation, and prediction-based hypotheses, while controlling for potential confounding differences in temporal

predictability and preparatory warning signals which might interact with attention.

Experiment 2 was an attempt to determine whether the pattern of attenuation effects observed in Experiment 1 would hold up when additional steps were taken to eliminate these confounding differences in temporal predictability between conditions. Therefore the design of Experiment 2 was intended to make all the conditions equally predictable. To the extent that this design succeeded, the self attenuation hypothesis predicted that self-initiated action effects would always be perceived as less intense compared to action effects produced by another person or a computer. The biological attenuation hypothesis predicted that both self- and other-initiated action effects would be attenuated compared to those produced by a computer. A strong version of the prediction based hypothesis predicted no difference in the judged speed of moves initiated by different agents, assuming the design succeeded in making all the conditions equally predictable.

The aim of Experiment 3 was to specifically manipulate predictability rather than eliminating it as a variable. By factorially combining variation in predictability with performance by the self or by computer, I hoped to tease apart the effects of predictability and self-agency on sensory attenuation. If sensory attenuation is a manifestation of a general process for predicting perceptions (i.e. the prediction based hypothesis), more predictable action effects should be attenuated compared to less predictable action effects, regardless of whether they were produced by a human or the computer.

EXPERIMENT 1

Experiment 1 was a conceptual replication of the second experiment in Weiss, Herwig, et al. (2011a), with the difference that the action effect in the present study was visual rather than auditory. Since the methods reported here closely adhered to theirs, I expected to replicate their pattern of results: attenuation of the speed of self-initiated moves compared to moves initiated by another person or the computer, while the latter two should not differ. If the self-initiated moves were attenuated compared to externally generated moves, this would support the hypothesis that sensory attenuation is a domain general phenomenon which similarly influences processing of auditory and visual action effects, while a failure to replicate would undermine this claim. An exact replication of the overall pattern of results reported by Weiss, Herwig, et al (2011a) would also support the self attenuation hypothesis, with the caveat that this design still confounded temporal predictability and attentional capture with agency.

Methods

Participants

Twenty-six healthy participants (3 male, 23 female, mean age 19.5, range 18 to 27) with normal or corrected vision were recruited from the psychology subject pool at Michigan State. A preliminary estimate of the effect size was obtained from a pilot sample ($N = 17$), and the final sample size was determined by a power analysis which estimated the final sample required for 90% power to find the observed difference between the Self and Computer conditions. All participants were naïve as to the

purpose of the experiment. Participants received course credits but no financial compensation for volunteering. Informed written consent was obtained from each participant prior to the experiment.

Design

The design of Experiment 1 had one within-subject factor, Agent, referring to the causal agent who initiated the action effect. The conditions were named Self, Other, and Computer.

Apparatus, stimuli and procedure

Following the consent procedure, participants were seated in front of a computer next to another person (a confederate of the experimenter). The confederate played the role of the other human actor and remained seated next to the naive participant for the entire experiment. Two lab assistants (one male and one female) alternated the role across participants. Seating assignments (left or right) were also counter-balanced across participants. Responses were made using a single keyboard that was shared by the two actors. The person on the left used the 'a' key to trigger action effects, and the person on the right used the '4' key on the number pad.

All the stimuli were programmed and presented using Matlab with the Psych toolbox extension. The main visual stimulus was a white square set against a black background with random white dots (see Figure 4). The white dots in the background moved when triggered by a key press or the computer (the action effect), while the square remained stationary at the center of the screen, giving the impression of a

square moving through outer space. The stimulus was programmed in this way to encourage fixation at the center of the screen, in order to avoid complications related to eye movements. The direction of the apparent motion (left or right) was counter-balanced across participants, but was held constant for all conditions within a given session. Following the approach of Sato (2008) and Weiss et al. (2011a), experimental sessions were divided into two phases: an acquisition phase, during which participants learned the action effect, and a test phase, during which sensory attenuation was assessed.

Acquisition phase. The purpose of the acquisition phase was to familiarize participants with the predicted action effect (i.e. moves at the standard speed). The acquisition phase was divided into two blocks: the Self block, during which participants practiced pressing their key to move the square, and the Other block, during which participants observed as the experimenter did the same. The block order was counterbalanced across participants.

The acquisition phase began with a stationary square-in-space display. After two seconds, a word in red font (either PARTICIPANT or EXPERIMENTER) appeared above the white square for 2 s as a warning that the Self block or the Other block, respectively, was about to begin (The words “participant” and “experimenter” were used rather than “self” and “other” to reduce confusion about which actor was being referred to).

For the Self block, participants were instructed to perform self-paced key presses at a comfortable rate of about once every 2-5 s. Each key press was followed 50 ms later by a move at the standard speed (20.40 deg/sec). Each move had a duration of 500 ms (30 frames on 60 Hz display). After each move, the square-in-outer-space

display was still again until the next key press. For the Other block, participants were instructed to observe closely as the experimenter did the same thing. Each block consisted of 200 trials. The acquisition phase usually lasted about 15 minutes.

Test phase. In the second part of the experiment participants performed a speed-discrimination task. As in the acquisition phase, the conditions were blocked so participants could focus their full attention on the respective conditions. The order of blocks was counterbalanced across participants, with the constraint that the Computer block always came after the Self block (explained below). A warning in red font at the start of each block indicated the condition (PARTICIPANT, EXPERIMENTER, or COMPUTER). The warning at the start of each remained for 2 s, and then disappeared.

Each trial began with the stationary square-in-space display. During the Self and Other blocks, the participant or experimenter, respectively, performed self-paced key presses to trigger the standard speed moves. There was then a 50 ms delay between each key press and the onset of the standard move. Following Weiss et al (2011a), the timing of events was different in the Computer condition. In the Computer condition, the white square turned green for 500 ms to warn of an upcoming move, which was followed 100 ms later by the standard speed move. In all conditions the standard move had a fixed speed of 20.40 deg/sec (at an approximate eye-to-screen distance of 57 cm) and lasted for 500 ms. The square-in-space was then stationary for a random interval from 800 to 1200 ms, followed by a comparison move at one of seven different speeds: 16.32, 17.68, 19.04, 20.40, 21.76, 23.12, or 24.49 deg/sec. The comparison move was always computer-initiated, in all conditions, and lasted for 500 ms. The range of comparison speeds was determined by pilot testing with the aim of covering the

whole range of psychometric functions. There were 20 repetitions of each comparison speed per condition, presented in random order. The comparison move was followed by another random 800 to 1200 ms delay with a static square-in-space display. Finally, a probe screen appeared asking “Did the square move faster on the first or second move?” Participants indicated which move they thought was faster by pressing '1' or '2'.

Immediately after the probe, the stationary square-in-space reappeared to await the next human or computer action. The human actors were told they should try to perform their key presses at a regular pace, waiting about 2 s from the end of the previous trial. In the Computer condition, the delay between the end of one trial and the green cue which warned of the next upcoming move was determined by randomly sampling (with replacement) from participants' own response latencies that were saved during the self block (which was the reason for always making the Self block first). Thus the general pace of the task was similar but not identical for the three conditions. The test phase usually lasted about 45 minutes.

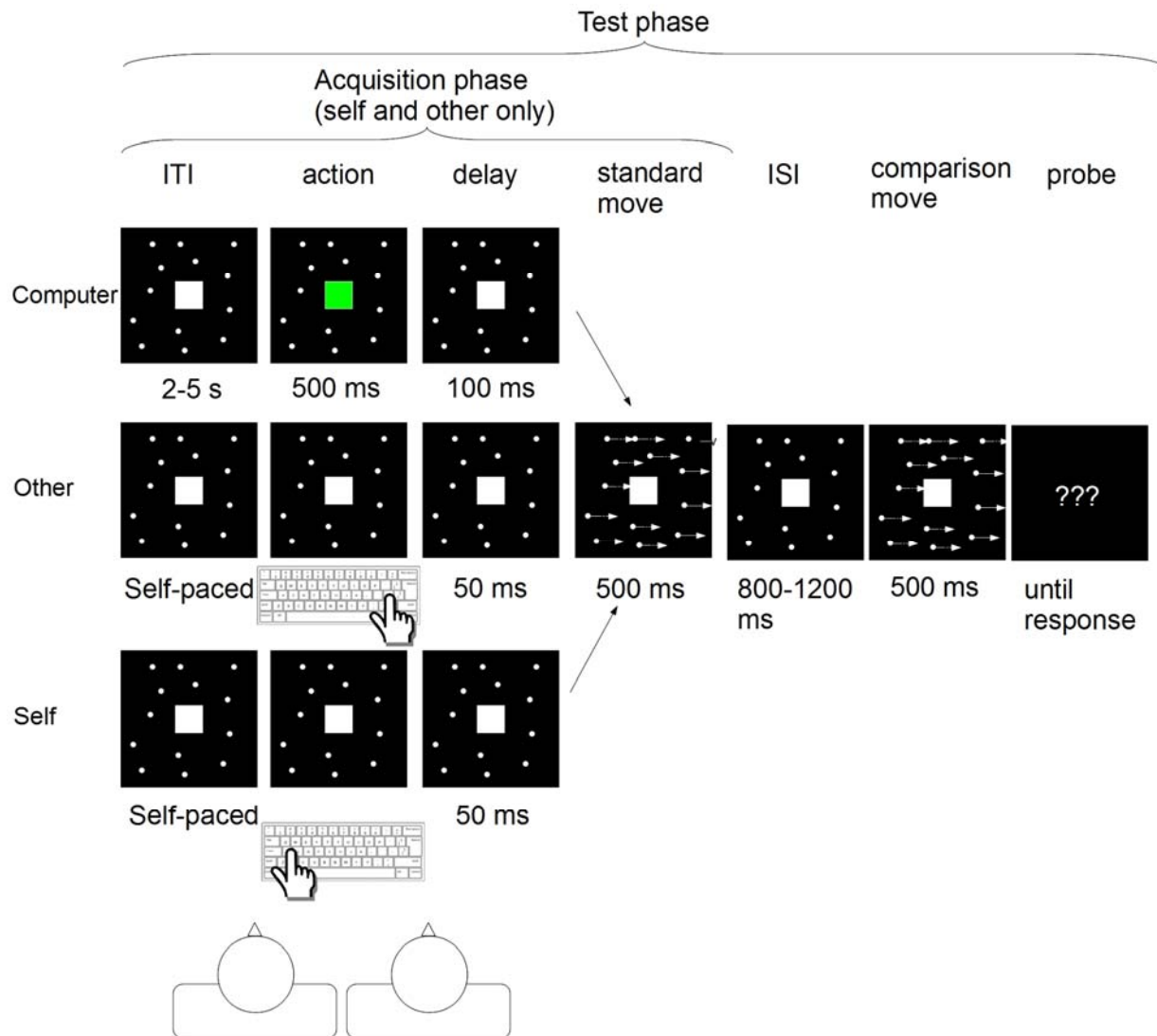


Figure 4. Stimuli for Experiment 1 (not to scale). For interpretation of references to color in this and all other figures, the reader is referred to the electronic version of this dissertation.

Data analysis

The proportion of 'second move faster' responses at each of the seven comparison speeds was calculated for each participant and condition and fit with a logistic function according to a maximum-likelihood procedure (Figure 5). The primary dependent measure of interest was the point of subjective equality (PSE) where the

comparison move was judged faster than the standard move on 50% of trials. Another measure of interest was the just noticeable difference (JND), or half the difference of comparison speeds judged faster on 75% versus 25% of trials. The JND was investigated because it carries information about the variability of speed perception in the different conditions.

The PSE and JND values were entered into single factor repeated measures analysis of variance (ANOVAs) with three levels, Self, Other, and Computer. The significance threshold was set to $p = .05$ for all tests. Since the expected direction of the main effect was known a priori, one-tailed t-tests were used to follow up on significant results on the omnibus test.

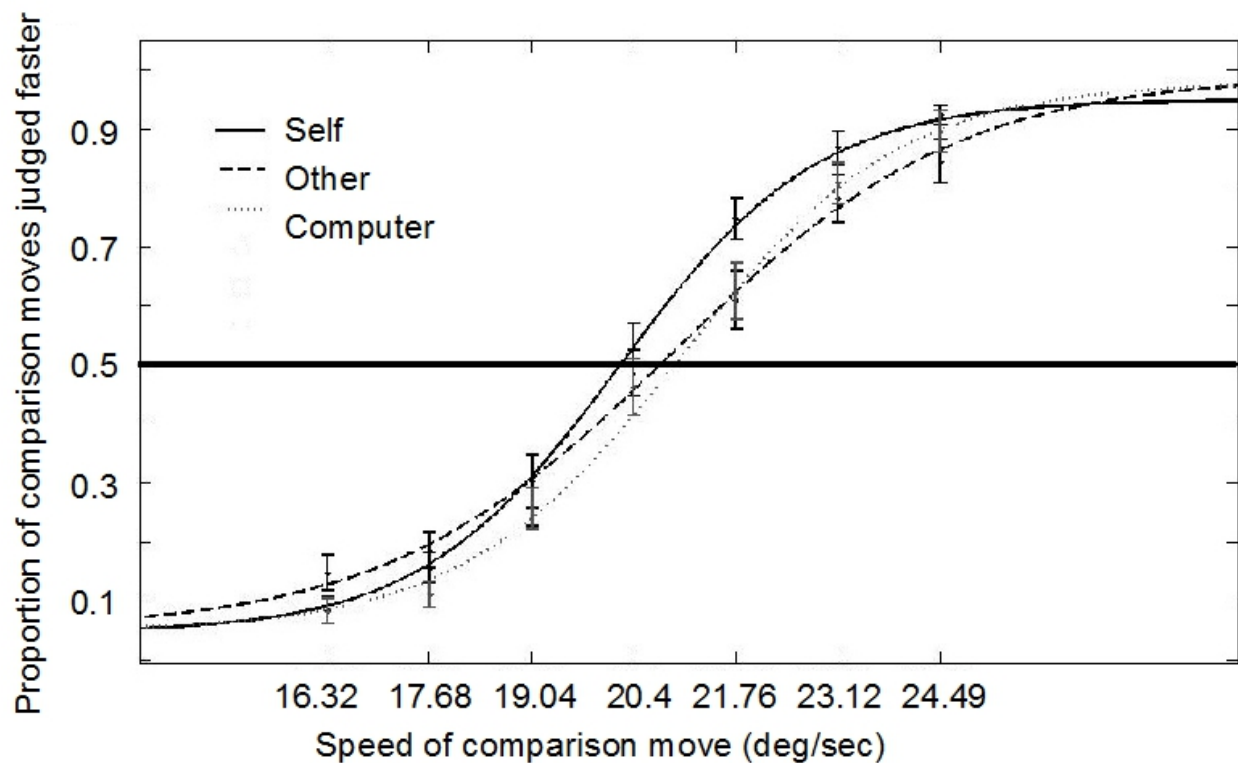


Figure 5. Group average psychometric function for each of the three conditions of Experiment 1. Error bars represent $\pm$ one standard error. The point of subjective equality is where the solid line crosses each curve.

Results and discussion

PSE. The analysis of PSE values showed a main effect of Agent, $F(2, 50) = 5.72$, $p = .01$, $\eta^2_G = .06$ (Figure 6A). PSE values in the Self condition were lower compared to the Other ($t(25) = -2.09$, $p = .02$) and Computer conditions ($t(25) = -3.33$, $p = .001$), but there was no significant difference between the latter two ($t(25) = -.72$, $p = .24$). Most but not all individuals followed the group pattern. Out of the 26 total participants, 21 had lower PSE values for Self compared to Computer, and 22 had lower PSE values for Self compared to Other.

JND. The analysis of JND values showed a marginally significant main effect of agent, $F(2, 50) = 2.86$, $p = .07$, $\eta^2_G = .04$ (see Figure 6B). The mean JND values were lowest for Self ($M = .80$, $SE = .07$ deg/sec) and highest for Other ($M = 1.09$, $SE = .14$ deg/sec), indicating that speed discriminations were, on average, slightly more difficult in the latter condition. This varied considerably across participants, however, and only 16 out of 26 participants had a lower JND for other than for self. A possible explanation for this difference is that, for some dyads, the onsets of the moves were less predictable in the Other condition than for Self. The JND for the computer condition was in between the Self and Other conditions but not significantly different from either ($p > .05$). As neither the PSE nor the JND values differed between the Other and Computer conditions, Experiment 1 provided no basis for concluding that action effects initiated by the Other were processed differently from those initiated by the Computer.

In all conditions, the mean JND was larger than the largest differences in the mean PSE values across conditions. This is only to make the point that the attenuation effects were quite small, and quite possibly below the (average) threshold of awareness.

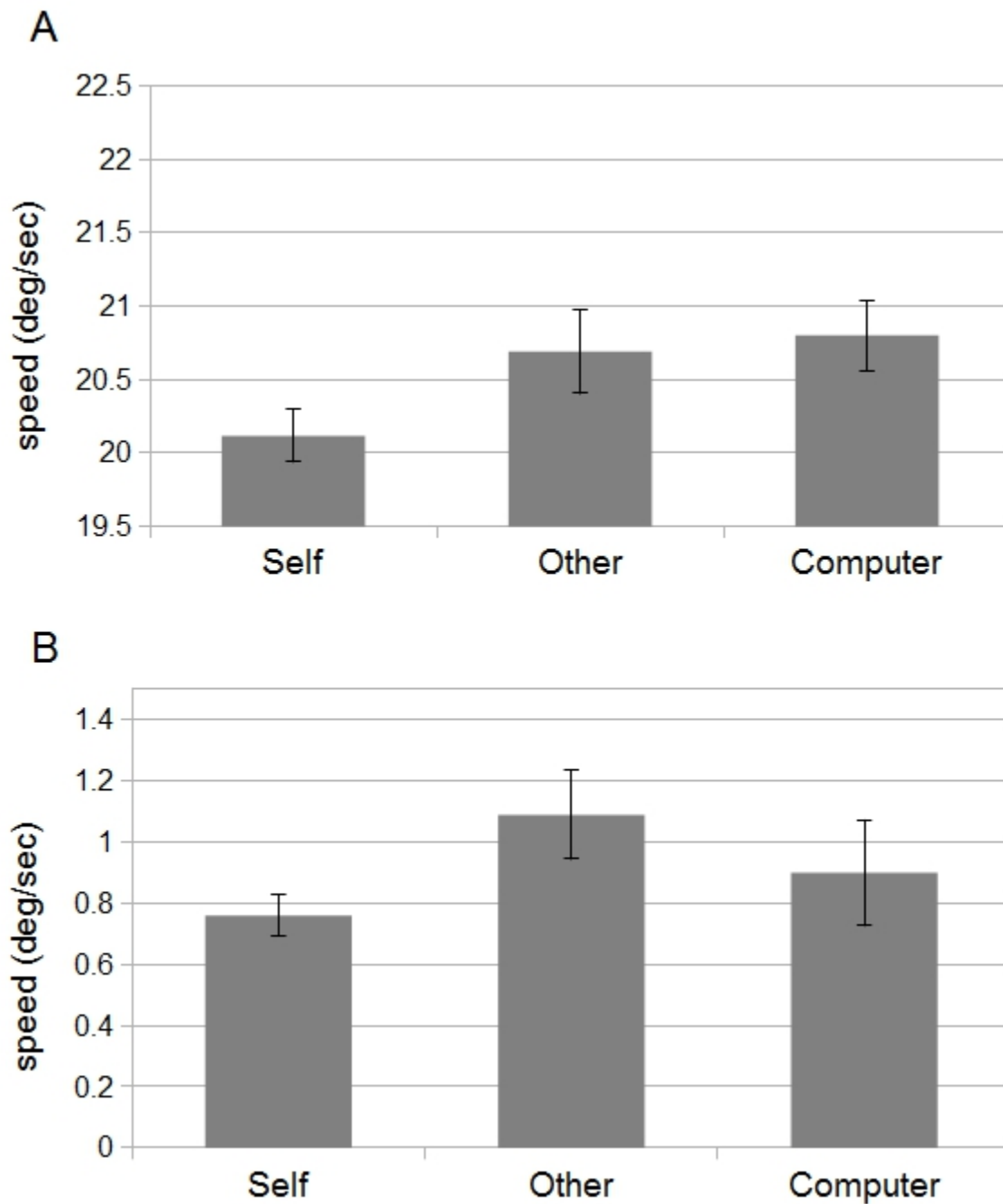


Figure 6. Means and standard errors for the (A) point of subjective equality and (B) just noticeable difference in the three conditions of Experiment 1.

Summary and conclusions. The pattern of results differed from Sato (2008) but agreed with Weiss et al. (2011a), on whose methods the present experiment was

based. Previously, Weiss et al. (2011) found that self-initiated auditory action effects were attenuated compared to objectively equivalent tones initiated by a computer or another person. Experiment 1 conceptually replicated this finding in the visual modality: Self-initiated moves were judged to be slower than moves initiated by another person or the computer program, while the latter two did not differ. This is consistent with the self attenuation hypothesis that sensory attenuation uniquely discriminates self-initiated action effects from external stimuli, whether human or non-human.

A caveat to these results is that the JND values were marginally lower for Self than Other, indicating that participants were slightly worse overall at judging small differences in the speeds of moving stimuli initiated by other people. I speculate the onset of the moves may have been less predictable (from the standpoint of the participant) in the Other condition. This is in line with the previous argument that minor differences in the temporal predictability of action effects may confound comparisons of the Self, Other, and Computer conditions when actions are self-paced. Furthermore, just like Weiss et al. (2011a), the visual warning prior to each move differed between the computer and the two human conditions. Therefore Experiment 1 does not settle whether differences in sensory attenuation across the three conditions were caused by interesting differences in how the human nervous system predicts action effects for different agents, or whether the pattern of results could be explained by differences in temporal predictability or attentional capture. The purpose of the next experiment was to make the three conditions more comparable with respect to temporal predictability and attention, to give a more definitive answer to this question.

EXPERIMENT 2

The purpose of Experiment 2 was to re-compare attenuation of the Self, Other, and Computer conditions, but with modifications to address some confounding differences in the timing of the actions and visual cues across conditions. In the previous experiment, the Self and Other conditions were self-paced, so the onset of the key presses in the Self condition may have been more temporally predictable. Furthermore, the Computer condition was preceded by a green warning light for 500 ms, followed by a 100 ms delay, followed by the onset of the move; whereas the human conditions had no visual warning signal, and the delay from the key press until the move was only 50 ms. To make the conditions more comparable in terms of temporal predictability and visual input, In Experiment 2, both human agents and the computer waited for a visual go signal before initiating a move. The go signal served as a warning that an action was about to occur, similarly to a traffic light. Thus, unlike Experiment 1, the visual input prior to the triggering action was identical in all conditions.

Each human key press or computer action was also immediately followed by a “command received” signal, consisting of a brief flash of color in which the square turned green for 50 ms. The command received signal served as an cue to orient attention to the upcoming move. The combination of the go signal and the command received signal was intended to make the conditions as similar as possible in terms of temporal predictability and the visual cues which oriented attention to the action effect. The original Computer condition from Experiment 1, with its much longer green signal and different timing, was also included for comparison and re-named the “Baseline”

condition to anchor cross-experiment comparisons. Another minor change from Experiment 1 was that a block of Computer trials was added to the acquisition period, again with the general aim of making the Self, Other, and Computer conditions more comparable.

If the changes just described eliminated previously observed differences between conditions, or otherwise altered the pattern of results, this would suggest that the previous results may have indeed been contaminated due to differences in temporal predictability and/or attention across conditions. This would be consistent with the prediction based hypothesis, i.e. it doesn't matter which agent initiated the action effect as long as the action effect was equivalently predictable in content and timing. Alternatively, if action effects were relatively attenuated for Self and Other compared to the Computer condition, this would support the biological attenuation hypothesis, consistent with Sato (2008). A third possibility is that the original self attenuation hypothesis is correct, consistent with Weiss et al. (2011a) and the results of Experiment 1. In this case only the Self condition should be attenuated.

Methods

Participants

Twenty-six healthy participants (nine males and 17 females, mean age 19.5, range 18-22) with normal or corrected vision were recruited from the psychology participant pool at Michigan State. The sample size matched Experiment 1, under the assumption that the effect size would be similar. Participants received course credits but

no financial compensation for volunteering. All were naïve as to the purpose of the experiment. Informed written consent was obtained from each participant prior to the experiment.

Design

Experiment 2 had one within-subject factor with four levels: Self, Other, Computer, and Baseline.

Apparatus, stimuli and procedure

The experimental apparatus, stimuli, and procedure were similar to Experiment 1, with a few modifications (see Figure 7). As before, the main visual stimulus was a white square set against a black background with random white dots. The white dots in the background moved when triggered by a key press or the computer (the action effect), while the square remained stationary at the center of the screen, giving the impression of a square moving through outer space. The major changes from the previous experiment were the additions of the go and command received signals. The go signal was a small black dot that appeared exactly at the center of the white square. The go signal disappeared after a key press or computer action was performed. Following each key press or computer action, the white square changed to a green color for 50 ms (the command received signal) until the onset of the standard move.

Acquisition phase. The acquisition phase consisted of six blocks of 75 trials each, three blocks each of training for the Self, Other, and Computer conditions. The block order was counterbalanced across participants using an ABCCBA type scheme with six

possible block orders. As before, a warning in red font appeared at the start of each block so participants knew whose turn it was to act. Participants were prompted to take a short break between blocks if they desired.

The task was the similar to the acquisition phase for Experiment 1, only instead of performing self-paced key presses the pace was controlled by the timing of the go signals. Each trial began with a stationary square-in-space display. Following a random inter-trial interval of 800-1200 ms, the go signal appeared in the center of the white square, and remained until a response was made. In the Self and Other blocks, the participant or confederate was told to respond as quickly as possible to the go signal, but not to respond before the go signal appeared. In the Computer block, the computer's response times were sampled with replacement from the distribution of previous participants' response times. In this way the computer's response times showed human-like variability.

After a response was registered, the go signal disappeared and the white square turned green (the "command received" signal). The square remained green for 50 ms until the move started. All the moves during the acquisition period were the same standard speed (20.4 deg/sec) and lasted for 500 ms. The delay between the end of one move and the next go signal was random between 800 and 1200 ms. The acquisition phase usually lasted about 15 minutes.

Test phase. The test phase consisted of eight blocks representing the four conditions: Self, Other, Computer, and Baseline. The first three conditions were modified from the previous experiment to include the go signal and command received signal. These changes only impacted the standard move (i.e. there was no go signal or

command received signal for the comparison moves, which were unaltered from Experiment 1). The baseline condition was identical to the original computer condition from Experiment 1. Block order was ABCDDCBA with counterbalancing of block order across participants. Participants were prompted to take short breaks in between blocks.

The task was the same as for the test phase in Experiment 1: Each standard speed move was followed by a comparison move at one of seven possible speeds: 16.32, 17.68, 19.04, 20.40, 21.76, 23.12, or 24.49 deg/sec. Participants performed a two alternative forced choice speed discrimination at the end of each trial, judging which of the two moves was faster. Participants pressed '1' if they believed the standard move was faster or '2' if they believed the comparison move was faster.

There were 56 trials per block, for a total of 16 repetitions of each of the seven comparison speeds per condition. The order of the comparison speeds was randomized within each block. The test phase lasted about 45 minutes.

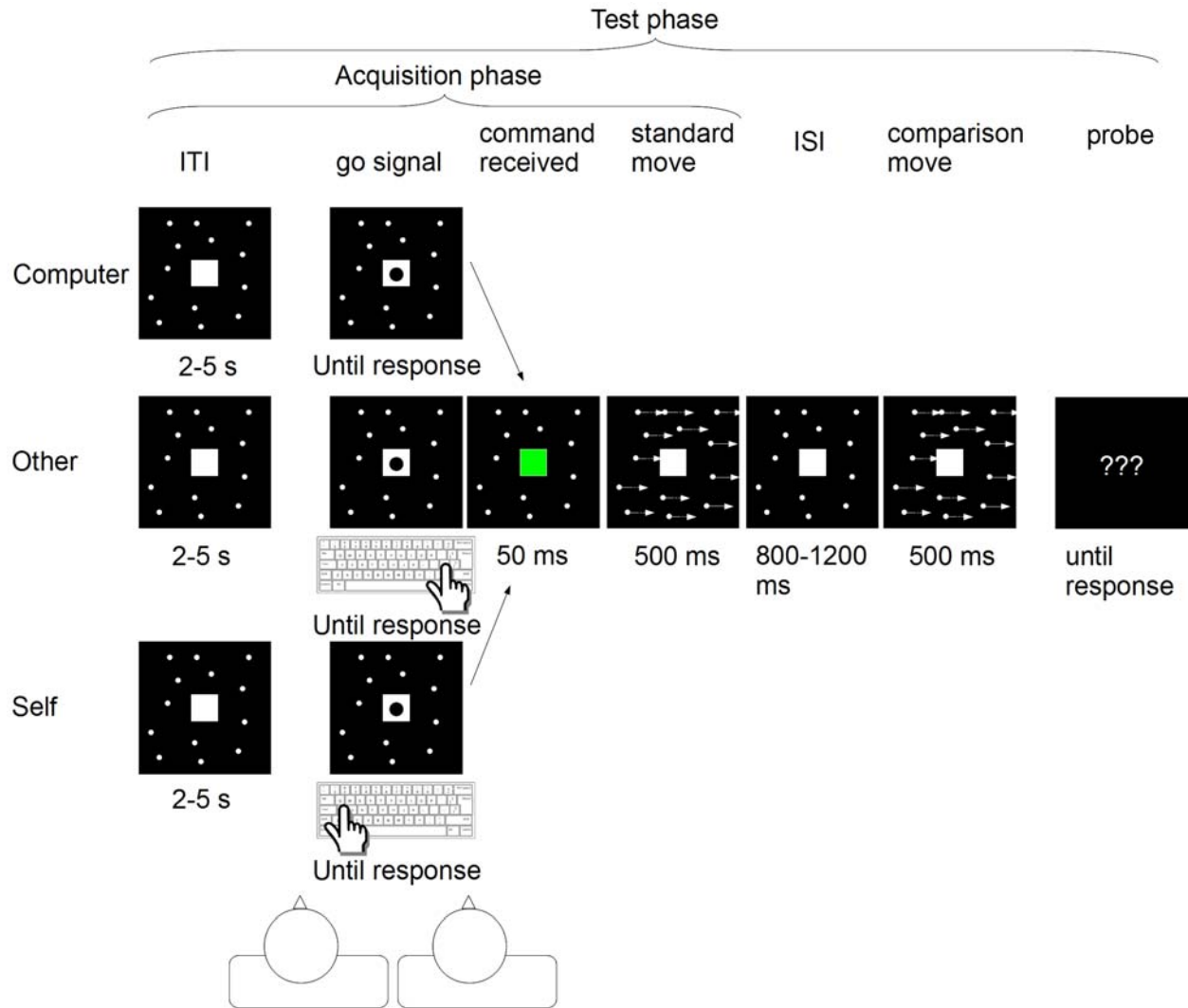


Figure 7. Stimuli for Experiment 2 (not to scale).

Data analysis

As before, PSE and JND values were extrapolated from a psychometric function fitted to each participant's data on each condition. The average psychometric function for each condition is shown in Figure 8. The PSE and JND values were entered into single factor repeated measures analysis of variance (ANOVAs) with four levels, Self, Other, Computer, and Baseline. The significance threshold was set to $p = .05$ for all

tests. One-tailed t-tests were used to test specific comparisons following a significant result on the omnibus test.

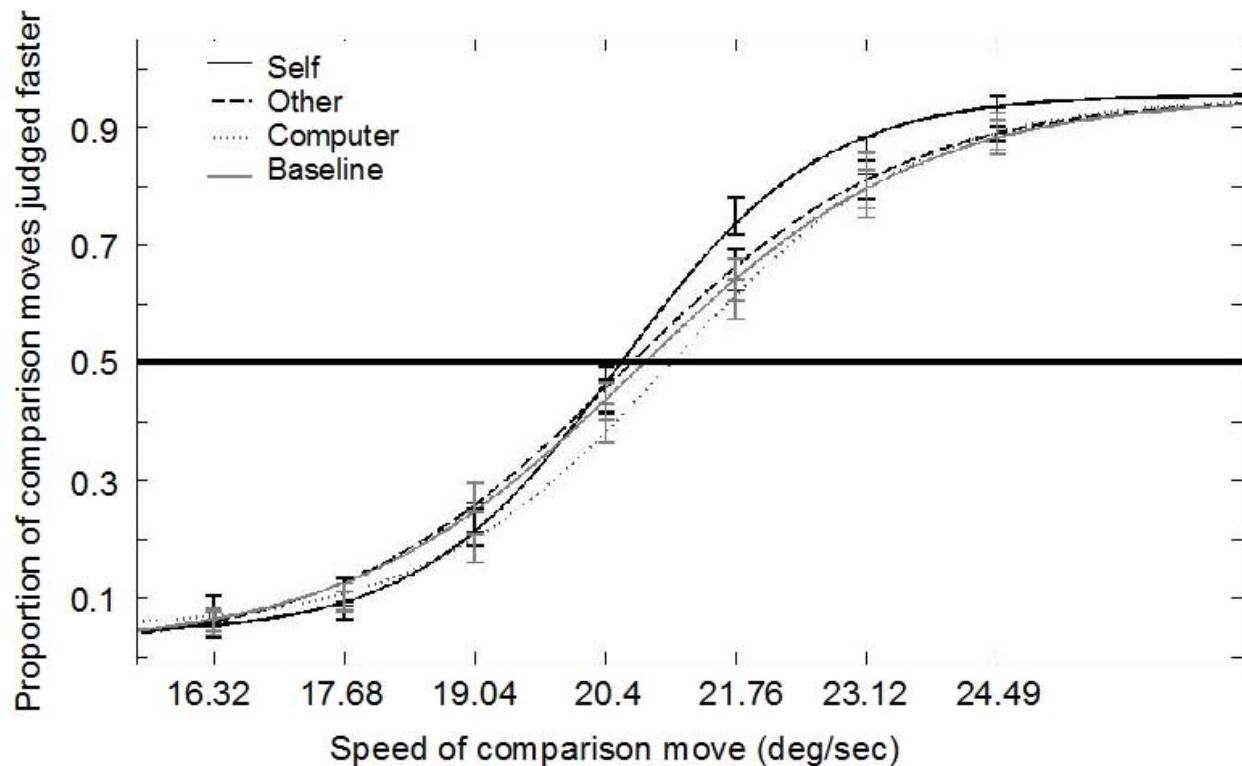


Figure 8. Group average psychometric function for each of the three conditions of Experiment 2. Error bars represent $\pm$ one standard error. The point of subjective equality is where the solid line crosses each curve.

Results and Discussion

PSE. The analysis of PSE values showed a main effect of Agent, $F(3, 75) = 4.93$, $p = .008$, $\eta^2_G = .03$ (see Figure 9A). Post-hoc paired sample t-tests (one-tailed) showed that the PSE values in the Self condition were significantly lower than every other condition: Self < Other, ($t(25) = -2.07$, $p = .02$), Self < Computer ($t(25) = -4.23$, $p < .001$), and Self < Baseline, $t(25) = -2.54$, $p = .009$. The Other condition was also attenuated compared to the Computer condition, $t(25) = -2.25$, $p = .02$, although it was not

significantly different from the Baseline (i.e. the original computer condition from Experiment 1), $t(25) = -.73$, $p = .24$. This may be because the lack of a go signal and different timing of the Baseline condition. Out of 26 total participants, 22 had a lower PSE for Self than for Computer, and 17 out of 26 had a lower PSE for Other than for Computer.

Notably, in Experiment 1 the PSE for the Self condition was less than the objective speed of the standard move (20.4 deg/sec), so the standard move was attenuated compared to its objective speed. In Experiment 2, by contrast, none of the conditions had a PSE less than 20.4 deg/sec, so the Self and Other conditions were only “attenuated” relative to the Computer condition. A mixed effects ANOVA on Experiments 1 and 2 showed a significant main effect of the experiment, $F(1, 50) = 1713.02$, $p < .001$, $\eta^2_G = .97$. The major differences between Experiments 1 and 2 were the additions of the go and command received signals prior to the standard move. The impact of these changes was to increase the PSE values in all conditions. Independent samples t-test revealed the PSE for the Self condition was significantly higher in Experiment 2 compared to Experiment 1, $t(50) = -1.95$, $p = .03$. The Other condition also trended higher in Experiment 2, but not significantly so, $t(50) = -.85$, $p = .20$. The Computer condition in Experiment 2 was slightly higher than the Baseline condition (which recall was the same as the Computer condition of Experiment 1), but not significantly different, $t(50) = -.31$, $p = .38$. The overall main effect Experiment 2 vs. Experiment 1 is consistent with the previous finding that presenting a brief visual cue 50 ms prior to a moving stimulus (the command received signal) increases speed judgments (Turatto et al. 2007). This can be interpreted as an increase in the perceived

speed of the standard move due to increased attention. It also explains why none of the conditions in Experiment 2 were attenuated compared to the objective speed. In every condition except the Baseline, there were two visual warnings prior to the standard move (the go signal and command received signal), but none prior to the comparison move. In other words, the warnings increased attention to the standard move relative to the comparison move. If attention increases perceived speed, this would tend to increase PSE values across the board.

JND. The analysis of JND values revealed no significant differences between conditions, $F(3, 75) = .47, p = .71, \eta^2_G = .006$ (see Figure 9B). Thus, the relative attenuation of self and other compared to computer were unlikely to be accounted for by differences in perceptual sensitivity. The absence of significant differences between the conditions is consistent with the overall goal of making the conditions equally predictable.

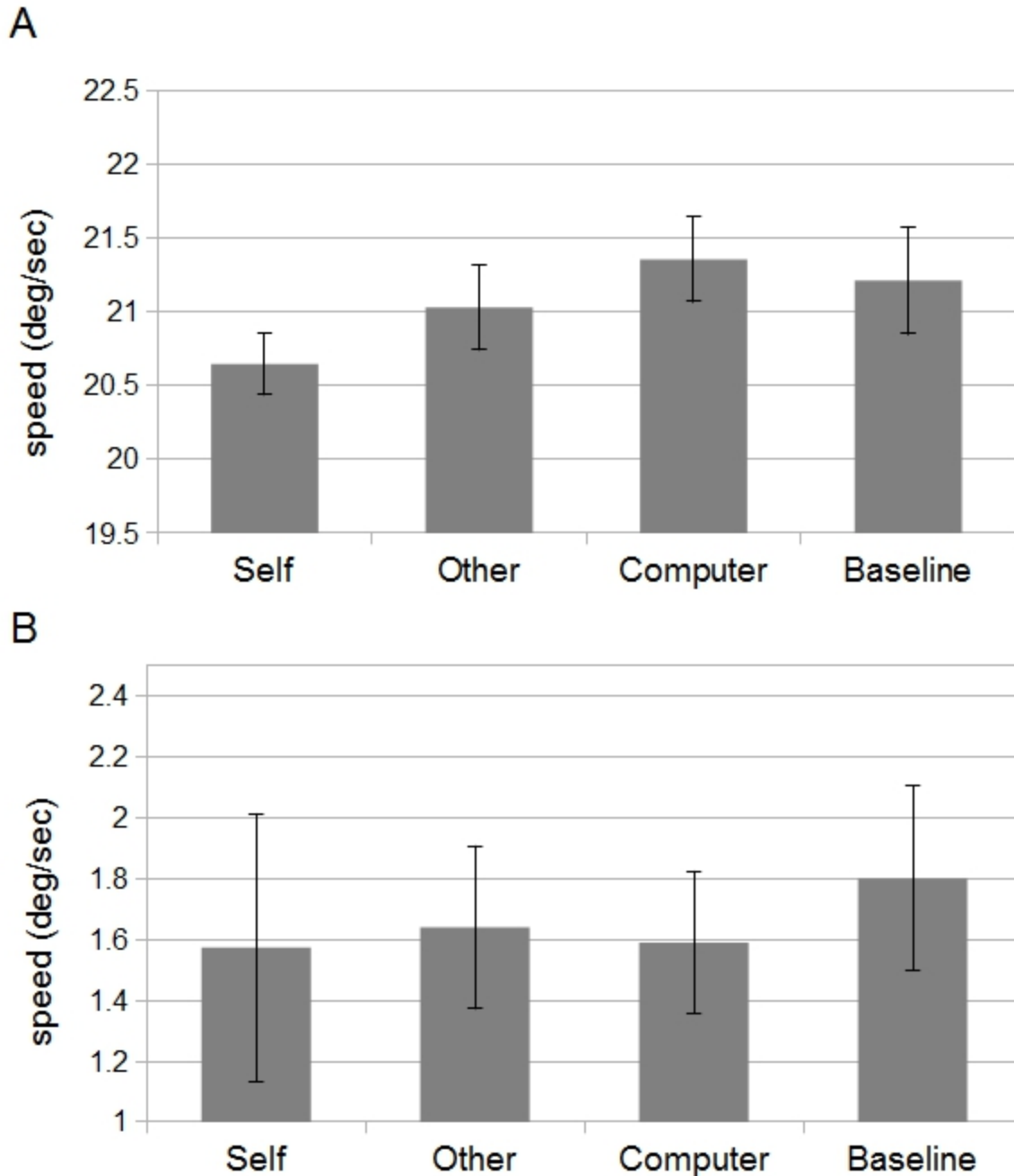


Figure 9. Means and standard errors of (A) the point of subjective equality and (B) just noticeable difference for each condition in Experiment 2.

Summary and conclusions. Attenuation of self-initiated moves persisted in Experiment 2 despite the additional controls put in place to match the conditions in terms of temporal predictability and visual warnings which might influence attention.

This suggests that attenuation of self-initiated action effects cannot be fully explained by differences in the temporal predictability of the action effect, or by differences in attention related to visual cues.

Although the moves initiated by the Other were not attenuated to the same degree as the Self, they were still significantly attenuated compared to the Computer condition. This is consistent with the results reported by Sato (2008). Thus, Experiments 1 and 2 produced patterns of results which resembled the findings reported by Weiss et al. (2011a) and Sato (2008) respectively. Where does this leave the self attenuation, biological attenuation, and prediction based hypotheses?

In both experiments the Self was the most attenuated condition, consistent with the argument that one's own intentional action effects are uniquely distinguished from all forms of external stimuli. This result indicates that a subset of the information contributing to the predictions which attenuate action effects is specific to action execution, and is therefore private information available only to the actor. This information could include efferent motor signals, a sense of agency, or proprioceptive cues only available in the Self condition.

Action effects initiated by another human were also distinguished from a computer agent, once controls were enacted to make the Computer and Other conditions equally predictable to the Self (Experiment 2). This supports the biological attenuation hypothesis, with the caveat that in most real world situations it is not possible to anticipate the timing of other agents' actions with such precision. Although efforts were made to ensure that all the conditions were equally predictable, the Computer condition was judged to be fastest on average. On a continuum of sensory

attenuation, action effects initiated by other human actors are in between self- and computer-initiated action effects. This suggests predictive forward models in humans are particularly tuned to intentional actions as they are performed by humans, although the current study cannot address what the critical difference between the other and computer conditions might be which explains this selectivity for human actions.

A general conclusion which can be drawn from the first two experiments is that sensory attenuation seems to be greater when more information is available to predict the action effect. A strong form of the prediction based hypothesis can be rejected insofar as predictability is not the only factor determining sensory attenuation. However, this does not mean predictability has no impact. The next experiment aimed to distinguish whether predictability also impacts attenuation, over and above the agent.

EXPERIMENT 3

In the previous experiments the self-initiated moves were consistently judged to be slower than the computer-initiated moves. This suggests executing an action contributes to sensory attenuation over and above the objective predictability of the action effect, contrary to the prediction based hypothesis. However, the impact of predictability itself could not be assessed because all the conditions were predictable. The purpose of Experiment 3 was to differentiate the contributions of executed motor commands (unique to the Self condition) and overall predictability (represented in purest form in the Computer condition) to sensory attenuation.

It has been argued that the adaptive value of sensory attenuation is to prioritize processing of novel or unexpected stimuli (Waszak, Cardoso-Leite, & Hughes, 2011). A proposed mechanism is that action preparation triggers a forward model which activates perceptual areas representing the predicted action effect. This prior activation makes the objective presence or absence of incoming sensory signals less discriminable (or intense), compared to situations with no prior predictions, or an incorrect prediction. An implication is that sensory attenuation should not be observed, or should be less pronounced, when an action effect turns out differently than expected, or when the statistical properties of an environment make it difficult to predict the action effect. For example, in a study by Cardoso-Leite, Mamassian, Schütz-Bosbach, and Waszak (2010), specific actions (left or right key presses) were associated with specific action effects (left or right tilted Gabor patches) during an initial acquisition phase. In the test phase, participants left and right key presses triggered faint Gabor patches only 50% of

the time, and reported the presence or absence of the patch. Perceptual sensitivity to the patches was less when the orientation was the same during the acquisition and test periods (congruent), compared to when the orientation changed (incongruent). Note that this effect cannot be explained as simple neural habituation to a particular orientation, because participants were required to perform approximately equal numbers of left and right key presses. Therefore this result suggests that action effects are attenuated to a greater degree when they are congruent with expectations. However, this study only considered self-initiated action effects. A missing piece of this puzzle is whether predictability similarly influences the intensity of externally generated stimuli. For example, if the speed of a computer-initiated move was judged differently depending on the predictability of the direction in which it moved, this would suggest that externally generated stimuli are also attenuated when they are anticipated, although perhaps not to the same degree as actions performed by biological agents, including oneself. If so, a more general principle might also be at work that the more novel or unexpected a sensory signal is, the more intensely it is perceived.

In Experiment 3, self- and computer-initiated action effects were compared when the action effects were either predictable or unpredictable. In the Predictable group, action effects were congruent with the triggering action on 80% of trials, whereas in the Unpredictable group, the action effect was congruent only 50% of the time – half and half. This design was intended to address whether the predictability of action effects also drives sensory attenuation, in addition to private motor information and agency. A strong version of the self attenuation hypothesis predicted that predictability and congruence should interact with the agent, such that only predictable and congruent

self-initiated moves should become attenuated. The prediction based hypothesis would predict that both self- and computer-initiated moves should be influenced by predictability and congruence. The Other condition was not included in order to keep the time commitment and number of trials asked of each participant to a manageable level, so there were no unique predictions associated with the biological attenuation hypothesis for this experiment.

Methods

Participants

An a priori power analysis determined that a sample of 82 participants would achieve 80% power to detect a “small” interaction within-between interaction between Agent and Predictability. In total, 88 healthy participants with normal or corrected vision were recruited in exchange for course credits. Of these participants, 44 were assigned to the Predictable group (mean age 20, range 18-31, 9 males and 35 females), and 44 more were assigned to the Unpredictable group (mean age 20.73, range 18-31, 15 males and 18 females). Two participants from the Unpredictable group were excluded from the final analysis after leaving the experiment early. All participants were naïve as to the purpose of the experiment. Informed written consent was obtained from each participant prior to the experiment.

Design

The design of Experiment 3 was $2 \times 2 \times 2$ with two within-subject factors, Agent (Self or Computer) and Congruence (Obey or Disobey), and one between-subjects factor, Predictability (Predictable or Unpredictable).

Apparatus, stimuli and procedure

After signing the consent form, participants were seated in front of a computer and shown the instructions for the experiment. To keep the total number of trials at a manageable level, only two levels of Agent were considered: Self and Computer. Therefore participants performed the task alone, rather than being paired with a confederate of the experimenter as before. Responses were made using a standard keyboard. Participants made the square move using two keys: the “a” key and the “4” key on the number keypad, and made their speed discrimination judgments with the “1” and “2” keys.

As in the previous two experiments, the main visual stimulus was a white square set against a black background with random white dots (Figure 10). The white dots in the background moved when triggered by a key press or the computer (the action effect), while the square remained stationary at the center of the screen, giving the impression of a square moving through outer space. However, this time the square could move in two directions, left or right.

As in Experiment 2, responses were prompted by a go signal. The go signal was a green bar which appeared on either the left or right side of the white square. The side on which the go signal appeared was random for each trial. During the Self blocks, participants pressed the “a” key whenever the go signal appeared on the left, and

pressed the “4” key whenever the go signal appeared on the right. The go signal was also shown during the Computer blocks to warn participants when the computer was about to trigger a move and to indicate, analogous to the Self blocks, which key the computer was about to “press”.

Each key press response or computer action made the square turn green for 50 ms (the command received signal), followed by a move at the standard speed which lasted 500 ms. Sometimes the standard move was in the same direction as the triggering key press – this was called the Obey condition. Other times the standard move was in the opposite direction from the key press or computer action – this was called the Disobey condition. The direction of the comparison move was always the same as the standard move.

Half the participants in the study were assigned to the predictable group, and half to the unpredictable group. The groups differed only in terms of the proportion of obey to disobey moves. The Predictable group underwent an acquisition period consisting of 100% obey moves, followed by a test period with 80% Obey and 20% Disobey moves. The Unpredictable group experienced 50% Obey and 50% Disobey trials during both the acquisition and test phases.

To increase the efficiency of PSE estimation, a staircase procedure was employed to adaptively change the speed of the comparison moves, in contrast to the method of constant stimuli used in Experiments 1 and 2. This is described in further detail under the procedure for the test phase.

Acquisition phase. The acquisition phase consisted of four blocks of 100 trials each, two blocks each of training for the Self and Computer conditions. The block order

was counterbalanced across participants using the ABBA method. The computer program prompted participants to take a short break between blocks if they desired. As before, a warning in red font appeared at the start of each block so participants knew whose turn it was to act.

The task was similar to the acquisition phases in the previous experiments. Like Experiment 2, the pace was controlled by go signals. Each trial began with a stationary square-in-space display. Next, a go signal appeared on the left or right side of the white square, and remained until a response was made. In the Self condition, participants were instructed to respond as quickly as possible with the appropriate key, but not to respond before the go signal appeared. In the Computer condition, the computer's response times were sampled with replacement from previous participants' response times.

After a response was registered, the go signal disappeared and the white square turned green (the “command received” signal). This was the same for the Self and Computer conditions. The square remained green for 50 ms until the move started. If the participant was in the Predictable group, the square always obeyed (i.e. the square moved the same direction as the key press). If the participant was in the Unpredictable group, the square obeyed on only half the trials, randomly selected. All the moves during the acquisition period were the same standard speed (20.4 deg/sec) and lasted for 500 ms. The delay between the end of one move and the next go signal was random between 800 and 1200 ms. The acquisition phase usually lasted about 15 minutes.

Test phase. The test phase consisted of two blocks (one for self, one for computer) of 250 trials each. The block order was counterbalanced across participants.

The computer program prompted participants to take a short break between blocks if they desired. As before, a warning in red font appeared at the start of each block so participants knew whose turn it was to act.

The task was similar to the test phases from the previous experiments. Following a go signal, either the participant or computer triggered a standard speed move. In the Predictable group, the square obeyed on 80% of trials, while in the unpredictable group, the square obeyed on 50% of trials. The Obey and Disobey moves were randomly ordered within each block of trials. The speed of the first standard move was always the same (20.4 deg/sec), and lasted 500 ms. The speed of the comparison move was systematically varied following the staircase procedure to zero in on the point of subjective equality. The comparison move was always in the same direction as the standard move, regardless of whether it was an Obey or Disobey move.

The staircase procedure which determined the speed of the comparison moves was controlled by Quest, an efficient algorithm for the estimation of psychophysical thresholds (Watson & Pelli, 1983). Quest begins with a prior guess and associated standard deviation for threshold (for PSE, the threshold is 50% correct). Then the observer is tested, and Quest saves the actual intensity of the stimulus along with whether the observer got it right. On this basis Quest re-estimates the threshold, and the cycle repeats. The final estimate of the PSE was the mean of the posterior probability distribution estimated by Quest (King-Smith, Grigsby, Vingrys, Benes, & Supowit, 1994). The total duration of the test phase was about 45 minutes.

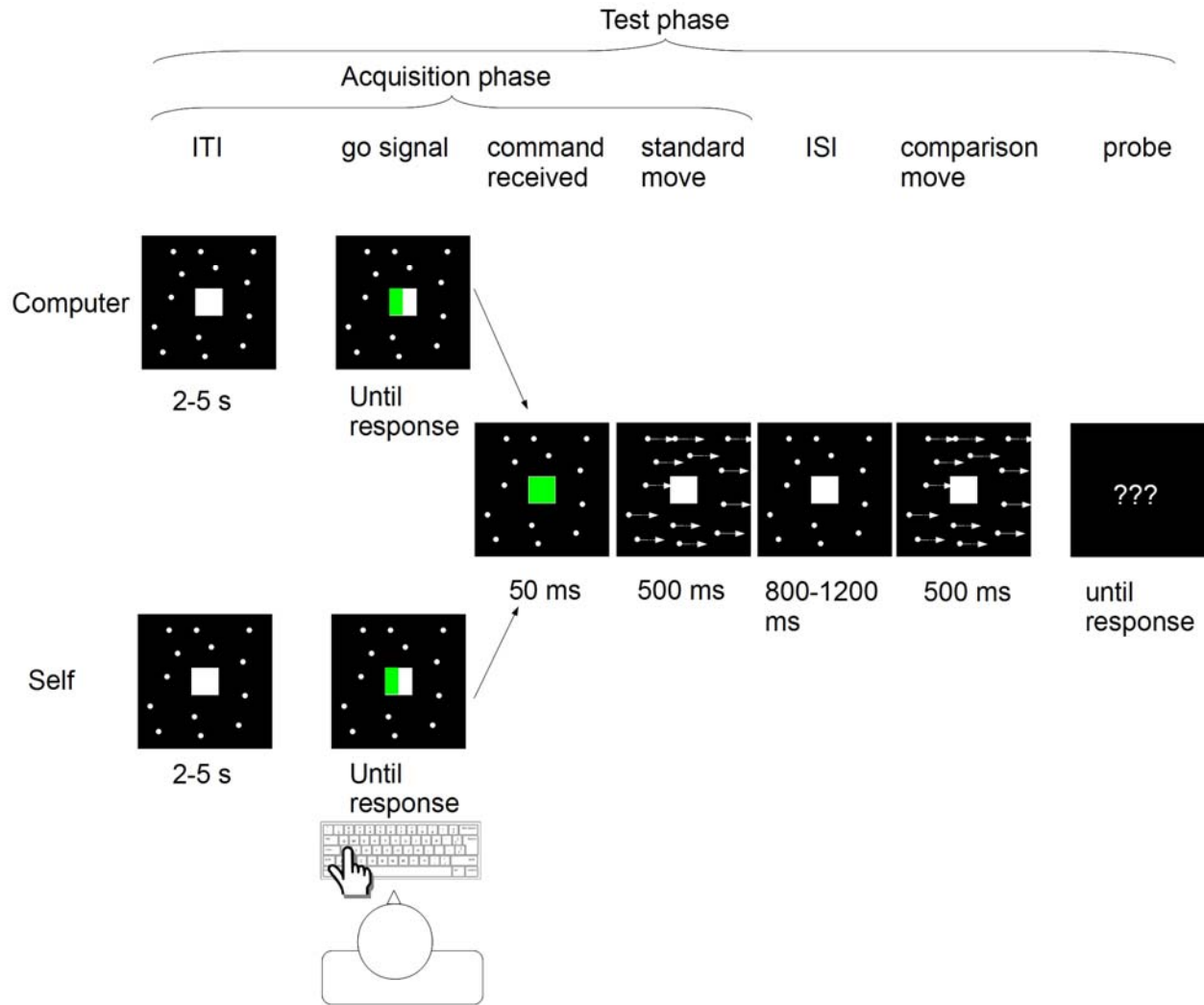


Figure 10. Stimuli for Experiment 3 (not to scale).

Data analysis

Because of the different procedure for estimating the PSE values compared to the previous experiments, this time the group psychometric functions and JND values could not be computed. The PSE values estimated by Quest were entered into a three factor mixed ANOVA with repeated measures on two factors, Agent (Self or Computer) and Congruence (Obey or Disobey). Predictability (Predictable or Unpredictable) was a between-subjects factor.

Results and Discussion

PSE. The mixed effects ANOVA showed no significant main effect of Agent, $F(1, 84) = 2.39, p = .13, \eta^2_G = .004$, Predictability, $F(1, 84) = .02, p = .88, \eta^2_G < .001$, or Congruence, $F(1, 84) = 1.22, p = .27, \eta^2_G < .001$. However, there were two significant interactions: Predictability x Agent, $F(1, 84) = 6.16, p = .02, \eta^2_G = .01$, and Predictability x Congruence, $F(1, 84) = 4.48, p = .04, \eta^2_G = .003$. The other interactions were not significant: Agent x Congruence, $F(1, 84) = .36, p = .55, \eta^2_G < .001$; Predictability x Agent x Congruence, $F(1, 84) = .28, p = .21, \eta^2_G < .001$. Means and standard errors for the predictable and unpredictable groups are shown in Figures 11A and 11B.

Post-hoc simple effects analyses using single –factor F tests were used to break down the two significant interactions. For Agent x Predictability, there was a significant effect of Agent in the Predictable group, $F(1, 43) = 12.31, p = .001, \eta^2_G = .02$, caused by attenuation of the Self compared to the Computer condition. The effect of Agent was not significant in the Unpredictable group, $F(1, 41) = .36, p = .55, \eta^2_G = .002$. For Congruence x Predictability, the effect of Congruence was not significant in the Predictable group, $F(1, 43) = .42, p = .62, \eta^2_G < .001$, but was significant in the Unpredictable group, $F(1, 41) = 6.04, p = .02, \eta^2_G = .006$, where the Disobey condition was judged faster than the Obey condition.

Similarly to Experiment 2, none of the conditions were attenuated compared to the objective speed of the comparison move (20.4 deg/sec). Again, this is most likely

because the visual warning signals (go signal and command received signal) prior to the standard move increased the PSE values across the board.

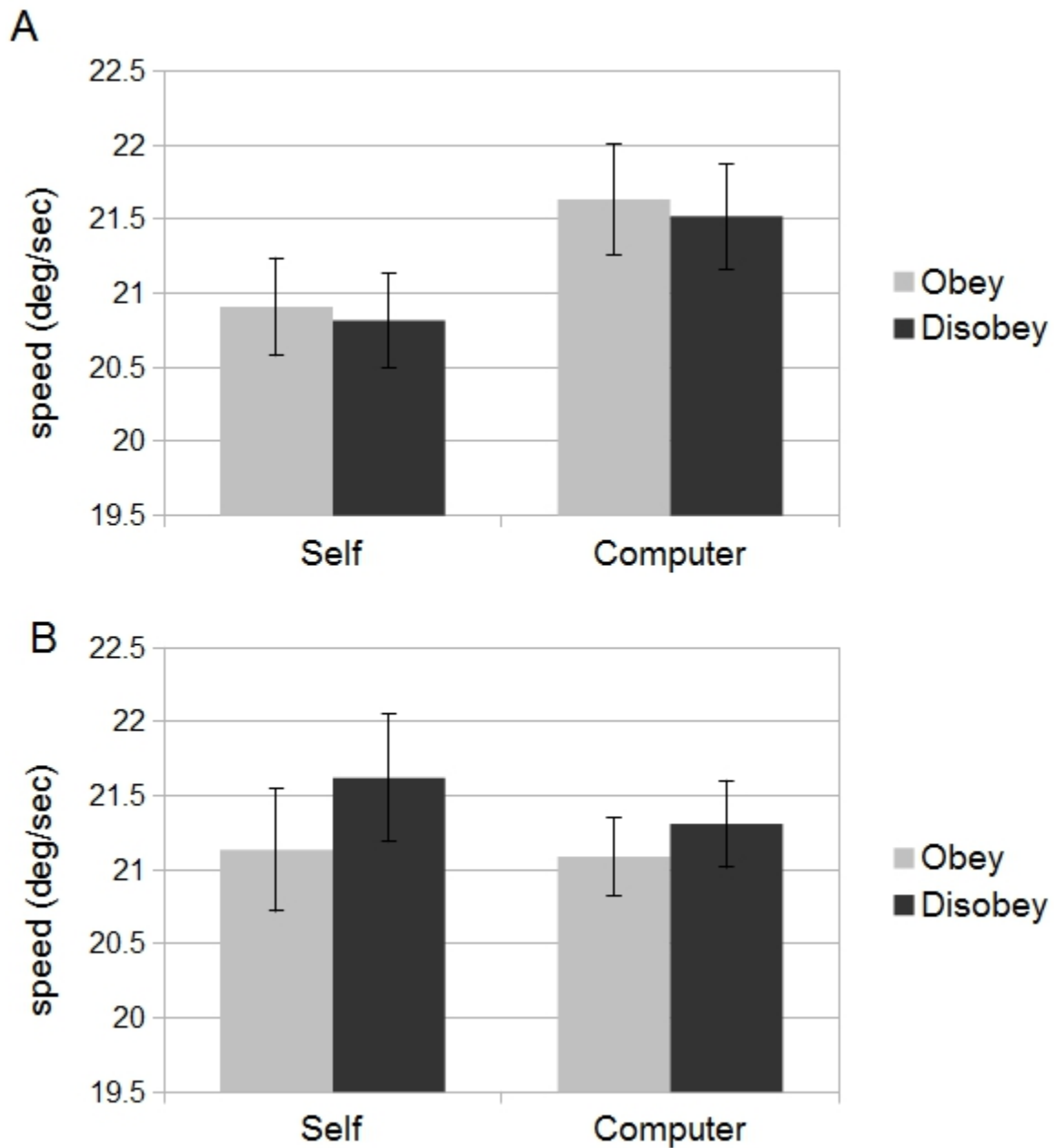


Figure 11. Means and standard errors of the point of subjective equality for each condition in the (A) Predictable group and (B) Unpredictable group in Experiment 3.

Summary and conclusions. The Predictability x Agent interaction suggests self-initiated action effects are only distinguishable from external stimuli in a context where action effects are predictable at above chance levels. This pattern of results suggests that a predictable action effect is necessary but not sufficient for sensory attenuation to occur. Rather, it seems sensory attenuation depends on a conjunction of human-like agency or intent with a predictable sensory consequence.

The Predictability x Congruence interaction is more difficult to interpret. Disobey moves were judged to be faster than Obey moves in the Unpredictable group where Obey and Disobey moves occurred with equal frequency. This is similar to a result reported in Weiss et al. (2011a) that self-initiated tones at a different-than-expected frequency were not attenuated to the same degree as tones previously associated with the action. Unlike in Weiss et al. (2011a) however, the different levels of Congruence in the Unpredictable group were equally probable during the acquisition and test phases. Thus the Congruence effect observed in the present study seems to have been related to spatial compatibility between the triggering action and the action effect, rather than how expected or unexpected the action effect was. However it is unclear why Congruence did not have a similar effect on the Predictable group – the Obey and Disobey conditions were equally attenuated in the Predictable/Self condition. This suggests that at least two potential action effects can be attenuated simultaneously. Meanwhile the effect of Congruence seems to be stronger when uncertainty is greater. This outcome might be explained by a difference in the level of attention to Obey moves across the Predictable and Unpredictable groups. The between-group comparison of Experiments 1 and 2 already suggested that stimulus-driven attentional capture

increases the perceived speed of moving objects. Expectations about probabilities can also guide attention (Summerfield & Egner, 2009). In the Predictable group, Obey moves were more probable than Disobey moves, so attention may have been more focused on this outcome. This may have caused the Obey moves to seem faster, thus cancelling out the effect of Congruence that was seen in the Unpredictable group.

GENERAL DISCUSSION

One of the hot topics of modern cognitive psychology and neuroscience is the notion of the predictive brain, covering all forms of anticipation, preparation, and “looking into the future” (Bubic, Von Cramon, & Shubotz, 2010). Sensory attenuation is one example of how the nervous system generates predictions and compares them to subsequent events. Although much is known about this type of processing, there are many open questions which need to be resolved to provide a fuller account of how the brain predicts the future.

Previous studies showed that self-initiated action effects are often judged to be less intense than externally generated effects. An explanation for this is that prediction of the sensory consequences of one’s own movements by a forward model can be used to attenuate the action effect (Bays et al., 2006). This account is supported by the fact that the extent to which self-initiated action effects are attenuated depends on the error between actually executed movements and sensory feedback (Blakemore et al. 1999). If the predictions by a forward model are triggered by executing actions, then sensory attenuation may be a unique property of intentional actions (the self attenuation hypothesis). On the other hand, a popular idea in recent decades has been that actions are at least partly represented in terms of their distal sensory consequences (Prinz, 1997). The discovery of mirror neurons in non-human primates which respond similarly during execution and observation of goal-directed actions (Rizzolatti & Craighero, 2004), along with fMRI and ERP studies on humans suggest we may covertly simulate and predict the actions of other actors (Ramnani & Miall, 2004; Sebanz, Knoblich, Prinz,

& Wascher, 2006). However, the question of whether actions initiated by another person are similarly attenuated by predictive forward models has been difficult to answer due to inconsistent results across studies (Sato, 2008; Weiss et al. 2011a).

There were three goals to the present study. The first was to conceptually replicate in the visual modality previous findings that self-initiated auditory and motor action effects are attenuated relative to computer-initiated effects. To my knowledge, no studies to date had compared attenuation of visual action effects produced by different agents using behavioral (rather than ERP) indices. This was accomplished in Experiment 1, adding weight to the argument that sensory attenuation is a general principle of self-action which influences different sense modalities in a similar way (as suggested in Engbert, Wohlschlagel, & Haggard, 2008). This does not imply that the mechanism must be the same in all cases. Specifically, the effect sizes reported here and in studies reporting attenuation of auditory action effects tend to be very small, whereas differences in ticklishness are rather more dramatic. It seems plausible that efferent motor information would play a larger role in predicting body position and somatosensory sensations, compared to visual or auditory action effects.

A second goal was to investigate whether observed actions performed by other people are attenuated in a similar fashion to self-initiated action effects. I considered three general hypotheses: the self attenuation hypothesis, the biological attenuation hypothesis, and the prediction based hypothesis. Experiment 1 showed attenuation of the judged speed of self-initiated moves compared to computer-initiated moves, but no difference between moves initiated by computer or another person. This outcome was consistent with the self attenuation hypothesis. However, a significant concern with past

studies (of which this was a replication) was that comparisons of action effects produced by different agents may have been confounded by differences in temporal predictability and/or differences in the warning signals prior to the action effect. Therefore in Experiment 2 the design was modified to better match the conditions in these terms. Differences in the magnitude of attenuation between the Self and Computer conditions remained, suggesting that sensory attenuation is not fully accounted for by differences in temporal predictability or preparatory visual warning signals. However, in contrast to Experiment 1, both Self and Other were attenuated compared to the Computer condition. This contradicts the specificity of attenuation to self-initiated actions reported in Weiss et al. (2011a) and Experiment 1 of the present study. The pattern observed in Experiment 2 constitutes evidence that predictive forward models can be applied to observed actions, with some selectivity for human actions, as would be required by the biological attenuation hypothesis. This outcome is consistent with Sato (2008), and with recent studies showing links between action perception and execution. For example, observing actions performed by others can prime motor responses (Brass, Bekkering, & Prinz, 2001), but the effect is smaller or nonexistent when the observed actor is a non-biological agent (Kilner, Paulignan, & Blakemore, 2003; Press, Bird, Flach, & Heyes, 2005; Tsai & Brass, 2007).

It is unclear what features distinguishing biological and non-biological agents lead to greater attenuation of observed action effects in the former case. One difference between the Computer and Other conditions was that the computer has no body. However, Sato (2008) reported attenuation of tones produced by another human, but not by a machine arm, and other studies have shown that attenuation of the self persists

even when aided by tools (Martikainen et al. 2005). Taken together, these suggest that embodiment matters less than the perception that the action was intentionally generated by a willful agent.

Although both the Self and Other condition were attenuated compared to the Computer condition, there was also a persistent difference between Self and Other, supporting the contention that the unique sensorimotor signals associated with self action bestow these action effects with a different experiential quality from other types of perceptions. These results indicate that sensory attenuation can be influenced by expectations transmitted to the agent via vision, audition, or some other sensory modality, but that motor or proprioceptive information within the agent also plays a role. This constitutes a rejection of the strongest version of the prediction based hypothesis, that objective predictability is the only factor which determines the degree of attenuation, and it also constitutes a rejection of a strong version of the biological attenuation hypothesis, given the greater attenuation of Self than Other. A recent study suggests top down knowledge such as a belief in one's efficacy as an agent also plays a role in sensory attenuation (Desantis, Weiss, Schütz-Bosbach, & Waszak, 2012).

Another finding from Experiment 2 was that the judged speed increased with the addition of visual warning signals prior to each move (the go signal and command received signal). This supports previous findings showing that visual cues which capture attention prior to presenting a moving object increase its perceived speed (Turatto et al., 2007). This highlights the importance of using the same visual cues to warn observers of upcoming action effects when comparing sensory attenuation for different agents.

Finally, in Experiment 3, the predictability of the action effect and its congruence with the triggering action were manipulated orthogonally to the agent, to investigate whether (and for whom) predictability modulates attenuation. Attenuation of self-initiated action effects was only observed when the direction of the action effect was predictable, and the Computer condition was never attenuated, regardless of predictability. This outcome suggests that neither self agency nor a predictable action effect alone are sufficient for sensory attenuation. Rather, sensory attenuation appears to be driven by a combination of human-like intentionality and a predictable action effect. Spatially incongruent (Disobey) action effects were judged to move faster than congruent (Obey) action effects only when Obey and Disobey moves were equally likely. This latter result was not anticipated, but may have been caused an increase in the level of attention to Obey moves in the Predictable condition.

In summary, the present experiments suggest sensory attenuation is particularly tuned to animate organisms, in line with the biological attenuation hypothesis, yet may be greater for self-initiated action effects than for the actions of others, in line with a weak version of the self attenuation hypothesis. Taken together, these results suggest sensory attenuation is driven by a combination of private information, which may include efferent motor signals, proprioceptive feedback, and a sense of agency, and more distal cues to upcoming action effects, such as visually transmitted information. Sensory attenuation is strongest when both types of cue are available to predict upcoming action effects, as in the Self condition.

A limitation of this research is that the PSE method of assessing sensory attenuation cannot distinguish between response bias and perceptual sensitivity.

Although it seems unlikely, if participants were biased towards judging the effects of their own actions as less intense independently of what they perceived, this would affect the PSEs. This shortcoming could be addressed in a future study by comparing thresholds for the detection of action effects produced by different agents.

Another potentially interesting future direction for this research involves comparing sensory attenuation of different agents in clinical populations with social deficits or a disordered sense of self, to investigate whether action effect prediction operates normally in these individuals. For example, it has been shown that schizophrenic populations do not attenuate the sensory consequences of their own actions in the normal manner (Blakemore, Smith, Steel, Johnstone, & Frith., 2000; Heinks-Maldonado et al., 2007). However, it remains to be seen whether this is due to a differences at the motor level, the integration of motor and distal perceptual signals, or both.

In conclusion, sensory attenuation results from internally generated predictions concerning the sensory consequences of actions, which are tuned to intentional actions performed by human agents, and especially tuned to actions by the self. This specialization suggests that among the many functions of “the predictive brain”, anticipating the consequences of one’s own actions is particularly important. One benefit of sensory attenuation may be a contribution to self-other distinctions (Weiss et al. 2011a). Another benefit is to prioritize processing of unexpected stimuli which may require a change in behavior (Waszak et al., 2011). Elucidating the mechanisms of sensory attenuation may contribute to a unified account of when, how, and why the brain predicts its future states.

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