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The *tau* effect put to the test of time

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Abstract

When equally spaced points on the skin of a blindfolded human individual are stimulated in rapid succession, stimuli separated by a shorter temporal interval are perceived as closer together in space than stimuli separated by a longer temporal interval. This perceptual illusion is known as the tactile variant of the *tau* effect. Here, a specific case of extinction of this phenomenon is discussed in the light of current theory. Psychophysical data of two blindfolded observers, tested under conditions of successive tactile stimulations of two points on the skin of the lower arm, with constant spacing and separated by two randomly varying temporal intervals, show that the *tau* effect occurs in the first trial blocks, and then vanishes over time. The data are discussed in the light of long-range interactions between somatosensory cortical neurons which, over a certain period of time, achieve a stable and reliable representation of tactile space independent of temporal variations. A neural state observer model for neural integration with temporal bias reduction is exploited to account for the individual data, and discussed in the light of previous explanations. The conclusions call for research into the conditions under which perceptual illusion may vanish, based on the hypothesis that such extinction studies could generate an even deeper insight into adaptive brain mechanisms than previously considered.

Introduction

Perceptual illusions are phenomena where a model-based prediction or perceptual hypothesis overrules the reality or true nature of an observed signal. They can teach us about adaptive brain mechanisms and other functional aspects of brain processing, as repeatedly shown for the case of visual perceptual illusions (e.g. Grossberg, 1914, Pinna & Reeves, 2006, Dresp, 1997, Francis & Grossberg, 1996). Yet, as many who have studied visual or other illusions over the years would probably agree, it sometimes happens that the more we are exposed to these illusions, the less we seem to be sensitive to them. In other words, their phenomenal strength often seems to fade with time and repeated exposure. While the conditions of their expression are extensively studied, as this special topical issue will no doubt once again show, few seem to be interested in conditions under which perceptual illusions may fade or vanish. This paper here discusses the specific case of extinction of a tactile variant of a perceptual illusion known as the *tau* effect, and its possible re-interpretation in the light of previous explanations.

The tau effect

The *tau* effect relates to a class of spatial perceptual illusions that has been observed with visual, auditory and tactile stimuli (see Goldreich, 2007 and Goldreich & Tong, 2013, for reviews). The *tau* effect occurs when observers are to judge the distance between successive stimulations in a sequence. When the distance in space from one stimulus to the next is

constant, and the time separating one stimulus from the next is also constant, subjects generally manage to correctly estimate the spatial distances. This is no longer the case when the spatial distance from one stimulus to the next is constant, but the time gap between the first stimulation and the following one varies. In fact, subjects then systematically misestimate the spatial distance between stimuli separated by shorter temporal intervals in terms of shorter spatial intervals.

Psychological relativity hypothesis

It has been argued that the spatial *tau* illusion and its temporal analogue, the *kappa* illusion, teach us that stimulus timing affects the perception of stimulus spacing and vice-versa and that this observation is to be interpreted in terms of the psychological equivalent of a consequence of the relation between time and space predicted by relativity theory (Gelb, 1914, Helson, 1930, Helson & King, 1931). Thus, our perceptual judgments of space and time would be determined interdependently. In his seminal paper on what he named the *tau* effect, Helson (1930) discusses a case of such “psychological relativity” on the example of a phenomenon “not due to imagination, suggestion, or attention” that “can be measured” and “obeys definite laws”. Referring to a tactile version of *tau*, where three distinct points on the hand or arm are touched lightly with the point of a pencil in quick succession, he observed an effect previously described by Gelb (1914), where the perceived spatial distance between stimulations depended on the time interval between the stimuli, not on the distance between the stimulated points on the skin.

Constant velocity hypothesis

The distance traveled by a moving object and the time taken by the object to travel that distance are linked by the physical laws of velocity. Thus, subsequent theoretical accounts for the *tau* and similar illusions have privileged explanations in terms of prior expectations of the perceptual system relative to objects moving in time and space. Such expectations may affect perceptual estimates of one or the other (time or space), as claimed in the so-called constant velocity hypothesis (Jones & Huang, 1982). According to this hypothesis, human spatial perception works on the basis of in-built prior expectations presuming constant velocity of objects that are moving uniformly in space. This constant velocity expectation would then explain why, when space is constant but not speed, misperception of spatial distance occurs as in the *tau* effect, or when speed is constant but not time, misperception of time occurs as in the *kappa* or S-effect (Suto, 1952), for example.

Low-speed expectation hypothesis

Perceptual misjudgments of spatial distance also occur when only two identically spaced stimuli not three, as in the original effect described by Helson (1930), are delivered in rapid succession to the skin. Then, the two stimuli are perceived as closer together the shorter the temporal interval between them. This observation may be more difficult to explain in terms of the constant velocity hypothesis. Tactile illusions including the *tau* and *kappa* effects have been reconsidered in this light. Instead of relating the *tau* effect to the laws of motion, a Bayesian approach (Goldreich, 2007, Goldreich & Tong, 2013) is exploited to simulate how low-speed priors could lead to the underestimation of spatial distance. The low-speed expectation hypothesis is based on the assumption that the brain would expect tactile stimuli to move slowly, as the particularly long signal integration times found in primate somatosensory cortex lead to suggest (e.g. Sripathi *et al*, 2006). The Bayesian model reaches

an optimal probabilistic inference by systematically associating spatial and temporal somatosensory information with a prior expectation for low-speed movement. Low-speed expectation would then lead to the underestimation of spatial distances between stimuli which follow each other more rapidly in time than expected. It is stated that the Bayesian approach accounts for *tau* as well as *kappa* effects (Goldreich & Tong, 2013).

How permanent is tau?

For how long can one's brain be fooled into using time as a measure for space? Whether the tau illusion is permanent for a given subject is, indeed, an open question. Sensory processes are subject to functional plasticity, which may express itself through significant changes with time or training, and it is not impossible that some perceptual illusions may fade or disappear when a subject is repeatedly stimulated for a certain length of time. To address this issue with regard to *tau*, we tested two blindfolded male observers on the least complex tactile variant of this effect, where only two locations on the skin are stimulated successively and repeatedly, with not more than two temporal intervals between stimuli, a longer one and a considerably shorter one. The spatial distance between the stimulated points always remains the same. The *tau* effect is expected to occur when the two stimuli separated by the shorter temporal interval are perceived as closer together than the two stimuli separated by the longer temporal interval.

Materials and Methods

Subject

Two male observers, 25 and 32 years old and naïve to the purpose of the study, volunteered to participate in this experiment.

Procedure

The observer was blindfolded and comfortably seated in an armchair, with the left arm, which was the one to be stimulated, resting on a table in front of the experimenter. Two small points, with a diameter of about one millimeter each and with a distance of eight centimeters between them, were drawn with a black magic marker on the skin of the inner side of the left arm while gently massaging the skin of the lower arm to distract the already blindfolded subject, who was not informed about this procedure. During the experiment, the two marked points on the skin were stimulated successively and always for about 250 milliseconds each by very gentle pressure through the tip of a wooden matchstick against the skin. The observers were not informed about the nature or purpose of the stimulations but they were told that they were going to be asked to estimate spatial distances between two successive and very gentle touches felt on the skin. The first trials were to prime the observer to a fixed arbitrary standard distance (modulus). He was informed that he will feel successive stimuli on his lower arm and given the instruction to spatially imagine the distance between the stimulated points as a straight line on his skin and associate this distance in his mind with a subjective magnitude of "100". Stimulations of the first point were separated from stimulations of the second point by a temporal interval of 2000 milliseconds. These "prime" trials were repeated until the observer declared that he was able to mentally represent the distance in terms of the arbitrary magnitude "100". After priming, the observer was told that he would now be stimulated again and that the spatial distance between the stimulation points could vary. He was instructed to produce a number after each stimulus pair that was to reflect the perceived magnitude of the distance between stimulation points as proportional to the

remembered magnitude of “100”, and it was precisely stated: “If you feel that the distance is the same as the one you have kept in mind, you should say “100”, but if you feel that the distance is, for example, half the one you have in mind, you should say “50”. Each so-called “test” trial consisted of two successive 250 millisecond stimulations separated by a temporal interval of about 400 milliseconds, which represents about 20% of the inter-stimulus interval of a prime trial. The true spatial distance (eight centimeters) between the two stimulated points was always the same. Ten blocks of ten stimulations were given to each of the two observers. The temporal separation between trial blocks was about 30 seconds. After initial priming, the number of prime trials (five per trial block) and test trials (five per trial block) was held constant. The temporal separation between a subject’s response and the next trial within a given block was constant (2000 milliseconds). A coach monitored the timing of events online by way of a stopwatch that counts milliseconds. A trained experimenter sitting next to the coach administered the stimulations based on hand signals from the coach. The first trial of each block was always a prime trial. Thereafter, the order of tests and primes varied randomly within and between trial blocks. The timed duration of a ten-block trial session after the priming phase was about six minutes (~360 seconds) per observer.

Results

Whenever a prime trial with the longer stimulus separation, to which the subjects were primed in the preliminary phase, occurred in a trial block, the subjects correctly estimated the spatial distance between the two stimulated points on the skin in terms of the standard subjective magnitude (modulus) of “100”. When a test trial with the much shorter temporal separation between stimuli occurred in a trial block, the subjects considerably underestimated the spatial distance between stimuli in the first trial blocks. The distance estimates from the test trials from each trial block were averaged per trial block and observer, and plotted as a function of the trial block number, following the order in which the blocks occurred in the experiment. These plots are shown here in Figures 1 and 2. The graphs show that, with the progression of trials in time, the distance estimates in test trials tend to become more veridical for both observers. For subject NB, they level off around a subjective magnitude of “90” (Figure 1), and for subject JD, they rejoin the standard level of the prime trial estimates with a constant subjective magnitude of “100” after eight trial blocks (Figure 2), which corresponds to a number of 40 test and 40 prime trials administered in random order. A power function provides a reasonably good fit for the data of each of the two subjects (see again Figures 1 and 2).

It is thus shown that the *tau* effect is present in both subjects at the beginning, but fades in one (subject NB) and vanishes completely in the other (subject JD) as the number of trials progresses in time. We account for this extinction of *tau* by an explanation in terms of long-range signal interactions in the brain achieving bias reduction and consolidation of a somatosensory representation of the spatially and temporally separated signal events (see the discussion here below). We modeled this kind of long-range neural integration for the real-world time scale of the experiment using a state observer model with bias reduction. The functional model properties are discussed in greater detail here below. Model simulations accounting for the individual psychophysical data are shown in Figures 3 and 4.

Discussion

In the particular case of *tau* described here, the illusion manifests itself in both subjects during the first trials of the experiment, as can be expected on the basis of results reported previously by others and cited here above. To account for this effect in the simplest

possible terms, we consider an interpretation in terms of temporal constraints on the spatio-temporal integration of successive tactile stimuli.

Temporal constraints on the “neural adequacy” of tactile representations

After having been primed repeatedly to a fixed time span between two tactile stimuli administered to two locations on the skin with a fixed spatial distance between them, the time span is suddenly drastically shortened on certain trials, while the spatial distance between the stimuli remains the same. Since the temporal sequences in the trials after initial priming are randomly selected and since the subject can neither anticipate the timing of these new events nor see with his two eyes where the subsequent stimulations are delivered on his skin, his brain is tricked into using time as a cue to estimate space because time is the only cue immediately available to him. This interpretation, though it may seem consistent with previous accounts in terms of low-speed expectancies or priors (cf. Goldreich, 2007, Goldreich et al, 3013), does not imply any in-built process that would lead the system to “expect” anything at this stage. It simply assumes that decisions are momentarily biased because the rules of the game have suddenly changed. As it turns out, the induced confusion between time and space does not last long. After a certain number of trials, the two subjects begin to produce more veridical distance estimates, which finally level off at, or near, the level of the subjective magnitude they were primed for. Rather than being fooled forever into relying on time as a perceptual cue to space, their brains adapt to the new situation. Time, or the total number of trials in time, is therefore critical in *tau* or, at least, the variant of the effect tested here. To consciously represent sensations in memory, the brain must be able to dissociate temporal from spatial signal contents (e.g. Dresch-Langley & Durup, 2009), but the mechanisms through which it manages to tell time and space apart are not yet understood. Concerning touch, there are at least four distinct sensory channels which contribute to the conscious perception of tactile signals. Psychophysical data on the functional tuning of these channels suggest that the integration of tactile stimuli into stable memory representations is subject to training or learning effects (Alluisi *et al*, 1965, Verillo & Gescheider, 1975, Mahrer & Miles, 1999, Craig & Belser, 2006, Dresch-Langley, 2013). The underlying cortical circuitry follows its own time. Brain data have shown that the integration times of neural structures in somatosensory cortex of primates are particularly slow (e.g. Sripati *et al*, 2006). The basal ganglia may be the subcortical network that mediates the long-latency interactions between different regions of somatosensory cortex, as suggested first by Libet and coworkers (e.g. 1979) and, subsequently, many others. Somatosensory neurons are, like the neurons in visual cortex, topologically organized into laminar circuits with a specific functional architecture, and activation in one channel can lead to the suppression of neighboring channels (e.g. Berwick *et al*, 2004). No single mechanism accounts for these long-range interactions but a series of processes, acting in concert to inhibit some channels and facilitate others. Moreover, tactile information from stimuli separated in space and time is projected across midline in the mammal brain (Wright *et al*, 1999, Zheng *et al*, 2001), which may slow down neural integration even more than previously considered. A stable brain representation of the distance between two successively stimulated receptors on the skin capable of overriding the distracting effect of other events, such as sudden variations in temporal intervals, is therefore likely to take a little while. The importance of the time gap that may separate integrated and stable cortical representations of events from their conscious perception has been emphasized repeatedly by Libet. Given the variability of the times the brain may need to achieve neural adequacy of an event representation and to generate a conscious response to that event (Libet *et al*, 1979, Libet, 2004), it becomes quite clear why most of our behavior is determined by the temporality of events, which affects all conscious judgment and decision making (see also

Dresp-Langley & Durup, 2009 and Dresp-Langley, 2012). In the experimental trials here, the time gap between a consolidated brain representation of a constant distance between two points stimulated on the skin and its veridical conscious perception would correspond to the number of trials needed by the subject to produce estimates independent of variations in temporal order. We suggest that the extinction of the tactile variant of the *tau* illusion reported here could be explained in terms of long-range consolidation of somatosensory cortical representations. Long-range interactions between cortical neurons may be the key to understanding how the brain manages to read sense into signals that are separated in space and time. To provide a model account for the behavioral data here (see Figures 3 and 4) in terms of neural integration over time, we exploited the functional properties of a state observer for bias reduction in neural and other systems, described previously (Schwaller *et al*, 2013).

A neural state observer for spatial integration as a function of time

State observers are both parsimonious, with a minimal number of parameters, and “universal” in the sense that they are designed to perform bias representation and/or bias reduction in any type of physical or living system. The model considered here exploits the time factor and represents bias as a temporally variable phenomenon. The bias function is then implemented in a state observer, which systematically associates signal input (or neural pulse activity) with a bias representation at a given moment in time. As demonstrated previously (Schwaller *et al*, 2013), the state observer achieves convergence towards an asymptotically stable and bias-free (neural) state representation proven by a Lyapunov function (see for example Sontag, 2008, for a review on the concept of Lyapunov stability). Thus, by incorporating time as a critical variable for generating what others have called neural adequacy of representation, our approach goes beyond neural engineering models of illusory phenomena, where state observer computations are exploited, but limited to representing bias as an internal property of neural systems (see for example, Grush, 2005). Under the assumption that bias is not permanent in time, we start from a biased neural representation (equation1). This bias function corresponds to the red curves in the graphs shown in Figures 3 and 4. The bias model is then implemented in the state observer to simulate how brains and other systems achieve long-range temporal integration and bias reduction with time ((equation2) and (equation3)). The mathematical properties of the model are summarized as follows:

We start with the temporal differential equation

$$\begin{aligned} \dot{x}_1(t) &= \Psi [x_1(t), u_1(t)] \\ \Psi [x_1(t), u_1(t)] &= -a x_1(t) + b u_1(t) \\ y(t) &= x_1(t) + \eta(t) \end{aligned} \tag{1}$$

with the parameters

$u_1(t)$: for signal input at time t

$x_1(t)$: for the state variable at time t

$\Psi [x_1(t), u_1(t)]$: for the temporal function that links signal input to a state observer

$\eta(t)$: for the magnitude of observer bias at time t

$y(t)$: for response output at time t

$a = 1/T_{sys}$: for the timing parameter

$b = a (1 - bias)$: for the gain parameter

To implement the functional model properties, the equation in (1) is linked to pulse activities (neural pulses) defined in terms of

$$\omega_o = 2\pi/T_o$$

wherein T_o defines the time constant of the neural state observer, leading to

$$x_1(t) = x_1(\tau), \quad \dot{x}_1(t) = \omega_o \dot{x}_1(\tau), \quad u_1(t) = u_1(\tau), \quad \eta(t) = \eta(\tau)$$

and

$$\begin{aligned} \dot{x}_1(\tau) &= \tilde{\Psi} [x_1(\tau), u_1(\tau)] \\ \tilde{\Psi} [x_1(\tau), u_1(\tau)] &= -\tilde{a} x_1(\tau) + \tilde{b} u_1(\tau) \\ y(\tau) &= x_1(\tau) + \eta(\tau) \\ \tilde{a} &= \frac{T_o}{T_{sys}} \frac{1}{2\pi} \\ \tilde{b} &= \frac{(1 - bias) a}{\omega_o} \end{aligned} \quad (2)$$

assuming $T_o = T_{sys}$ the temporal dynamics of the observer are defined as constant.

This gives the neural state observer structure:

$$\begin{aligned} \dot{\hat{x}}_1(\tau) &= I_0(\tau) + 2 \Delta y(\tau) + \tilde{\Psi} [\hat{x}_1(\tau), u_1(\tau)] \\ \dot{I}_0(\tau) &= \Delta y(\tau) \\ \Delta y(\tau) &= y(\tau) - \hat{x}_1(\tau) \\ \tilde{\Psi} [\hat{x}_1(\tau), u_1(\tau)] &= -\tilde{a} \hat{x}_1(\tau) + \tilde{b} u_1(\tau) \end{aligned} \quad (3)$$

with the parameters

$\hat{x}_1(\tau)$: for the observer output

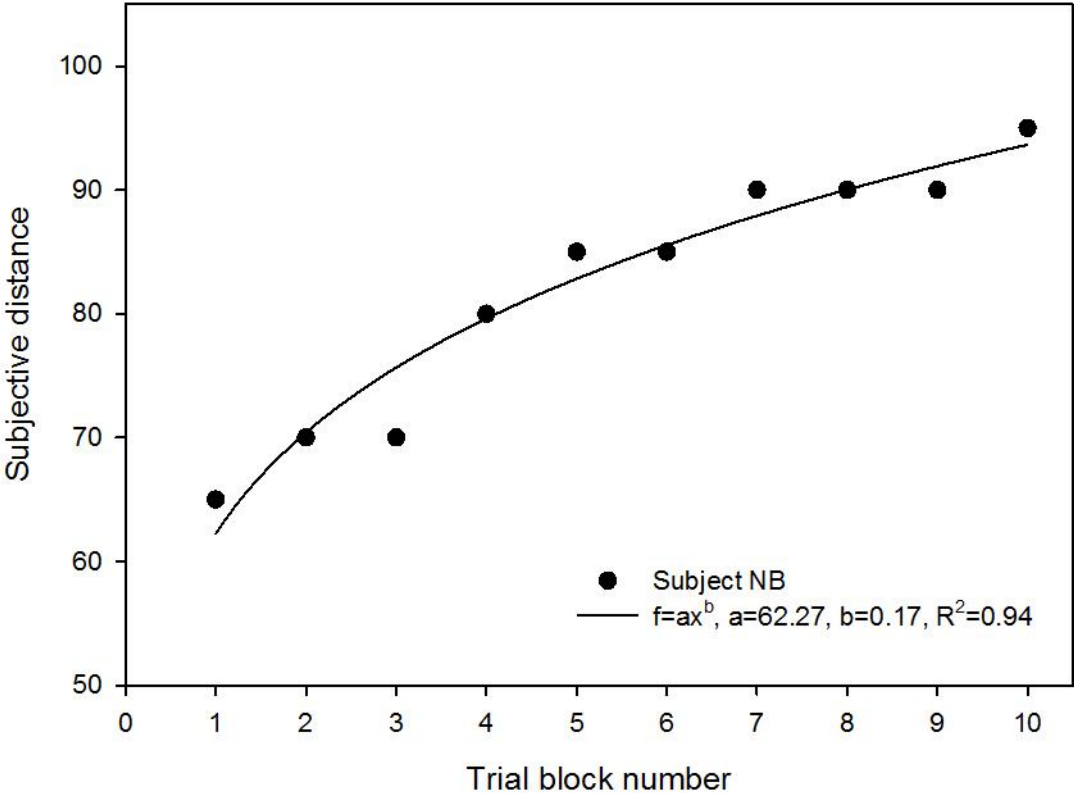
$I_0(\tau)$: for compensated bias

$\Delta y(\tau)$: for the state differences

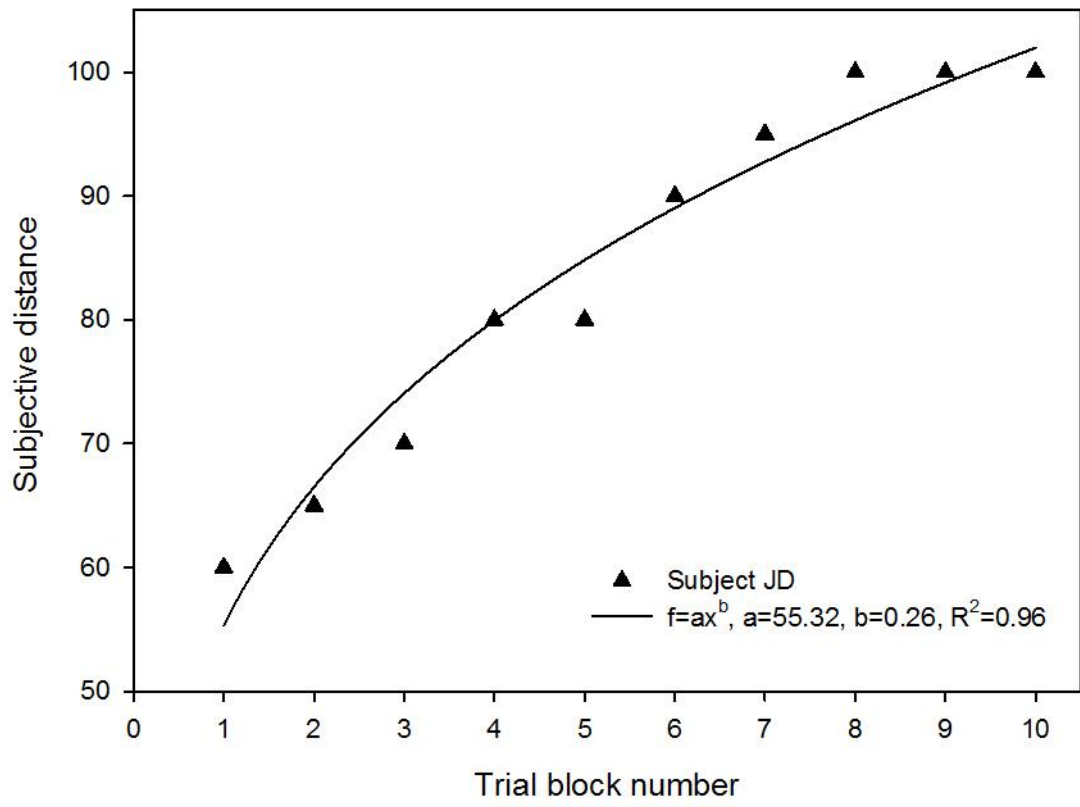
Conclusions

The possible reduction or extinction of the *tau* illusion with repeated stimulations in the course of a restricted time period offers new insights into potential mechanisms underlying the genesis of this particular illusion, and possibly other space-time illusions. This leads to argue for a new line of research into perceptual illusions considering not only the conditions of their expression but also, and maybe above all, the conditions of their possible extinction. This may, as suggested here, shed a fresh light on adaptive brain mechanisms and stimulate new modeling approaches. Clearly, if the phenomenal attributes of perceptual illusions are to tell us about how perception permits our brains to adapt to the world, then the phenomenal characteristics of their vanishing from our perception should tell us at least as much and maybe even more.

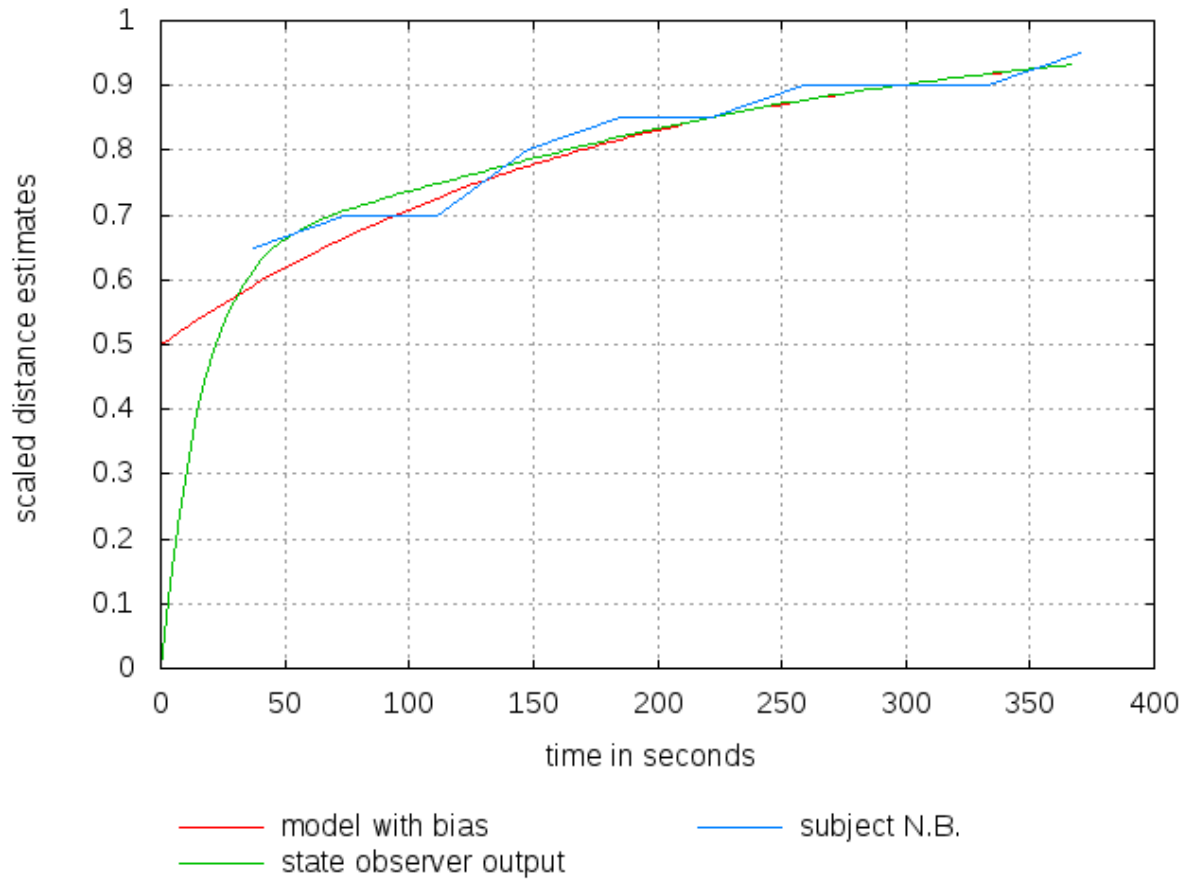
Figures



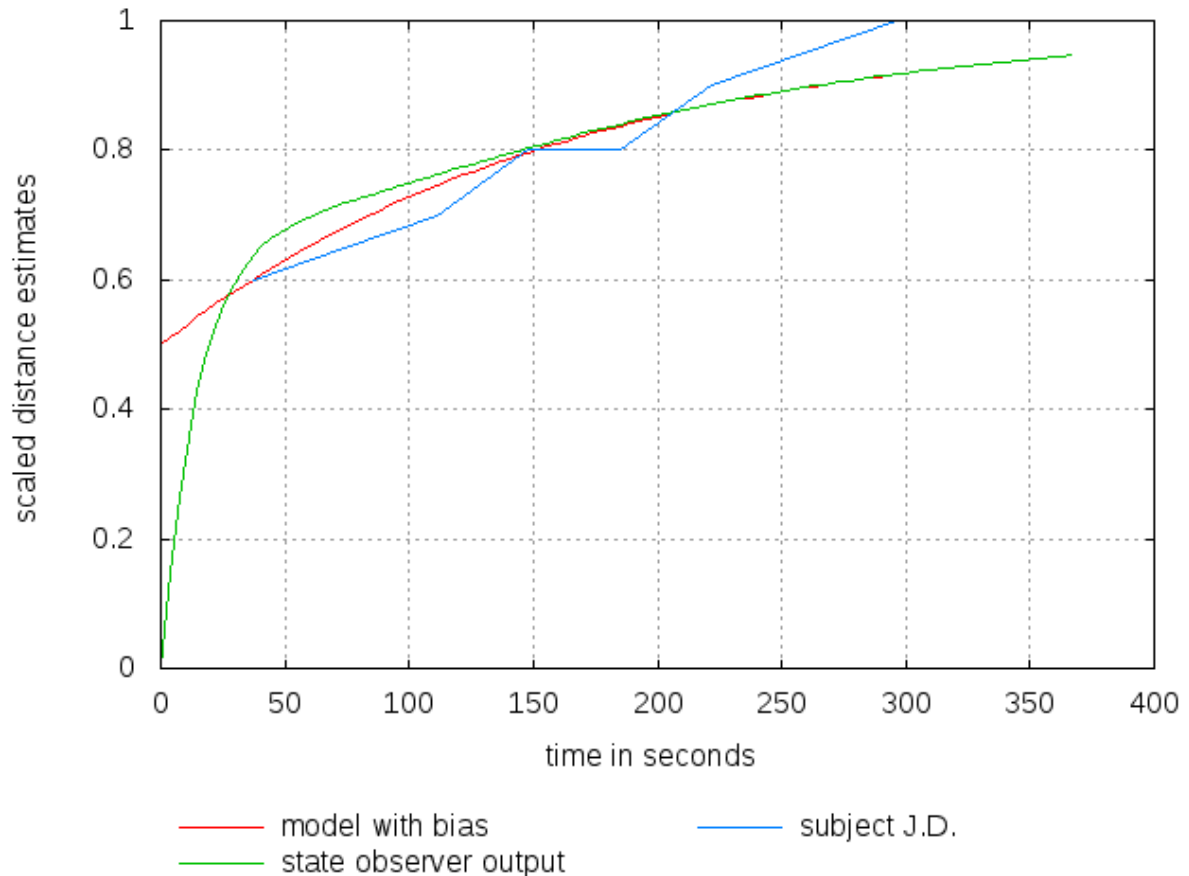
1a



1b



2a



2b

Figure captions

Figures 1a and b

Distance estimates (subjective magnitudes) from the test trials from each trial block, averaged per trial block and observer and plotted as a function of the trial block number in the order in which they occurred in time. With the progression of the trials, the distance estimates in the test trials tend to become more veridical for both observers. For subject NB, they level off around a subjective magnitude of “90” (Figure 1a), and for subject JD, they rejoin the level of the prime trial estimates, with a constant subjective magnitude of “100” after eight trial blocks (Figure 1b). A power function provides a reasonably good fit for the data of each subject.

Figures 2a and b

Model simulations exploiting the functional properties of a state observer for bias reduction in neural and other systems are shown here to account for the individual data, represented by the blue curves, of subjects NB (Figure 2a) and JD (Figure 2b). The time factor is taken into account and bias (perceptual or other) is represented as a temporally variable phenomenon, shown in the red curves. The bias function is then implemented in a state observer which systematically associates signal input, or neural pulse activity, with a bias representation at a given moment in time. The output function of the state observer is represented by the green curves.

References

- E. A. Alluisi, B. B. Morgan *jr* and G. R. Hawkes (1965) Masking of cutaneous sensations in multiple stimulus presentations. *Perceptual and Motor Skills*, **20**, 39–45.
- J. Berwick, P. Redgrave, M. Jones, N. Hewson-Stoate, J. Martindale, D. Johnston and J. E. W. Mayhew (2004) Integration of neural responses originating from different regions of the cortical somatosensory map. *Brain Research*, **1030**, 284-293.
- J. C. Craig and A. N. Belser (2006) The crossed-hands deficit in tactile temporal-order judgments: the effect of training. *Perception*, **35**, 1561–1572.
- B. Dresp (1997) On illusory contours and their functional significance. *Current Psychology of Cognition*, **16**, 489-518.
- B. Dresp-Langley (2012) Why the brain knows more than we do: Non-conscious representations and their role in the construction of conscious experience. *Brain Sciences*, **2(1)**, 1-21.
- B. Dresp-Langley (2013) Generic properties of curvature sensing by vision and touch. *Computational and Mathematical Methods in Medecine*, **Article ID 634168**, 1-7.
- B. Dresp-Langley and J. Durup, J (2009) A plastic temporal code for conscious state generation in the brain. *Neural Plasticity*, **Article ID 482696**, 1-15.
- G. Francis and S. Grossberg (1996). Cortical dynamics of form and motion integration: Persistence, apparent motion, and illusory contours. *Vision Research*, **36**, 149-173.
- H. Helson (1930) The tau effect - an example of psychological relativity? *Science*, **71**, 536.
- H. Helson and S. M. King, S. M. (1931) The tau effect: an example of psychological relativity. *Journal of Experimental Psychology* **14** (3), 202–217. Doi: 10.1037/h0071164.
- B. Jones and Y. L. Huang (1982) Space-time dependencies in psychophysical judgments of extent and duration: algebraic models of the tau and kappa effects. *Psychological Bulletin* , **91** (1), 128–142.
- A. Gelb (1914) Versuche auf dem Gebiet der Zeit- und Raumanschauung. In F. Schumann (Ed), *Bericht über den VI. Kongress für experimentelle Psychologie*: Göttingen, pp. 36–42.
- D. Goldreich (2007) A Bayesian perceptual model replicates the cutaneous rabbit and other tactile spatiotemporal illusions. *PloS ONE* **2** (3), e333.
- D. Goldreich and J. Tong (2013) Prediction, postdiction, and perceptual length contraction: A Bayesian low-speed prior captures the cutaneous rabbit and related illusions. *Frontiers in Psychology*, **4**, 221.
- B. Libet, W. Elwood, B. Feinstein and D. K. Pearl (1979) Subjective referral of the timing for a conscious sensory experience: a functional role for the somatosensory-specific projection system in man. *Brain*, **102**, 193–224.

- B. Libet (2004) *Mind Time - The Temporal Factor in Consciousness*. Harvard University Press.
- P. Mahrer and C. Miles (1999) Memorial and strategic determinants of tactile recency. *Journal of Experimental Psychology: Learning, Memory and Cognition*, **25**, 630–643.
- R. T. Verrillo and G. A. Gescheider (1975) Enhancement and summation in the perception of two successive vibrotactile stimuli. *Perception and Psychophysics*, **18**, 128–36.
- B. Pinna and A. Reeves (2006) Lighting, backlighting and the laws of figurality in the watercolor illusion. *Spatial Vision*, **19**, 341-373.
- Grossberg, S. (2014) The visual world as illusion: The ones we know and the ones we don't. In A. Shapiro and D. Todorovic (Eds.) *Oxford Compendium of Visual Illusions*. Oxford, United Kingdom: Oxford University Press.
- R. Grush (2005) Internal models and the construction of time: generalizing from *state* estimation to *trajectory* estimation to address temporal features of perception, including temporal illusions. *Journal of Neural Engineering*, **2**, 209-218.
- B. Schwaller, D. Ensminger, J. Ragot, and B. Dresp-Langley (2013) State estimates for a class of non-linear systems. *International Journal of Applied Mathematics and Computer Science*, **23(2)**, 1-16.
- E. D. Sontag (2008) Input to state stability: basic concepts and results. *Lecture Notes in Mathematics (Springer)*, **1932**, 163-220.
- A. P. Sripathi, T. Yoshioka, P. Denchev, S. S. Hsiao and K. O. Johnson (2006) Spatiotemporal receptive fields of peripheral afferents and cortical area 3b and 1 neurons in the primate somatosensory system. *The Journal of Neuroscience*, **26** (7), 2101-2114.
- Y. Suto (1952) The effect of space on time estimation (S-effect) in tactual space. *Japanese Journal of Psychology*, **22**, 45–57.
- A. K. Wright, L. Norrie, C. A. Ingham, E. A. M. Hutton and G. W. Arbuthnott (1999) Double anterograde tracing of outputs from adjacent columns of rat somatosensory cortex. Neostriatal projection patterns and terminal ultrastructure. *Neuroscience*, **88**, 119–133.
- Y. Zheng, D. Johnston, J. Berwick, J. Mayhew (2001) Signal source separation in the analysis of neural activity in brain. *NeuroImage*, **13**, 447– 458.