

NEURAL CORRELATES OF SENSATION AND PERFORMANCE AS REVEALED BY NEUROIMAGING STUDIES

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Abstract

We present and discuss evidence on how neurophysiological measures of brain activation supplied by various neuroimaging methods relate to stimulus intensity, on the one hand, and subjective experience, in particular, sensory magnitudes and measures of performance (like speed or accuracy of response), on the other. We argue that in modern neurophysiology, the functional relation between the stimulus intensity and the neural response is largely neglected in favor of research on higher-order, cognitive processing. In turn, physiological psychology has yet little to say about the relation between neural activity and the sensory magnitude. Moreover, most current work in neuroscience lacks a parametric examination along the entire line stimulus-neural activity-sensation. A deeper insight into the nature of the functional relationship between the intensity of sensation and the magnitude of nervous activity in the brain requires an interdisciplinary effort made by neurophysiology, physiological psychology and sensory psychophysics.

The issue of how neural events representing the world around us are coupled to subjective experience has a long history in philosophy, biology, and psychology. In his seminal work *Elemente der Psychophysik. Teil II.*, Gustav Theodor Fechner (1860) introduced *inner*, complementary to outer sensory, psychophysics (*innere Psychophysik*) as an experimental discipline that deals with the nature of the functional relationship between the intensity of sensation and the magnitude of nervous activity in the brain. Today, this domain is most appropriately assigned to physiological and, more generally, biological psychology. It is noteworthy that the Fechnerian conception misses an important link between the stimulus intensity and neural activity, the issue that still remains unresolved in modern neuroscience. For a better understanding of the relations that exist between the environment, brain, and sensory experience, a proper combination of sensory psychophysics and neuroimaging is required. Psychophysics may benefit from this combination while building neurobiologically sound psychophysical models and theories. In turn, brain imaging can make use of psychophysics to disentangle the impact of diverse, often confounded experimental variables on brain activation,

and understand how activation measures relate to specific stimulation protocols and subjective states, thereby significantly improving behavioral relevance and diagnostic value of imaging.

At present, imaging modalities most commonly used in neuroscience include (multi-channel) electro- and magnetoencephalography, EEG and MEG, (event-related) functional magnetic resonance imaging, fMRI, and positron emission tomography, PET. Current neuroimaging research, however, is mainly concerned with the higher-order cognitive and emotional processing, motor activity and their brain topography (e.g., Nichols & Newsome, 1999) rather than with the lawful functional relations existing between the stimulus, neural activation, and sensation. Neurophysiologically and psychophysically oriented studies each look at links between either a neural or an overt (behavioral) response, and a stimulus. Little systematic research has been done specifically on how changes in the stimulus magnitude alter a neural response to it and how these two relate to the sensory magnitude or performance on that stimulus (cf. the sensory aggregate model proposed by Baird, 1997, who also gives a concise review on neural psychophysics). In this paper, we focus on this work, in which at least some of the relations are traced. In the next section, we briefly outline the major advantages of and limitations on a combination of psychophysics and brain imaging.

Combining psychophysics and neuroimaging

Combining brain imaging with psychophysics brings about several important advantages, but it has a number of restrictions as well. The main advantages are as follows.

- a. Imaging provides a variety of measures of brain function like the magnitude of neural response, its frequency spectrum, latency, and location in the brain, as well as their changes over time (the time-course) or along a stimulus dimension.
- b. These measures reflect an aggregate (cell population) activity as opposed to the activity of single neurons as provided, for example, by single-cell recording.
- c. In most cases, an imaging epoch/trial can be made event-related, synchronized with a stimulus or response.
- d. Basically, imaging can allow one to study processes related to sensory representation of a stimulus and to response generation and execution.
- e. Moreover, it may help examine the interactions (e.g., feedback and –forward connections, synchronies) that exist between distinct (sub)cortical regions involved.

The limitations and difficulties while measuring neural activity in psychophysical tasks are both technical and theoretical. Some of them are listed below.

- a. Many imaging techniques are either indirect (like fMRI, in which changes in cerebral blood oxygenation are used to index neural activation) or reflecting activation of several, not clearly separable neuronal substructures.
- b. Some experimental psychophysical and imaging protocols may hardly be compatible. For example, while in psychophysics a set of stimuli are typically employed, the need for data averaging often makes it necessary during imaging session to drastically reduce the number of distinct stimuli presented. Also, because an overt (verbal and a verbal) response usually used in psychophysical experiments may affect neural activation, it is often avoided in imaging studies.
- c. So far, no agreement exists about which measure of neural activity, if any, would best indicate the changes both in the stimulus magnitude and in its sensory counterpart (Baird, 1997).

- d. In psychophysics, a change along one stimulus dimension (e.g., wavelength) can generate distinct changes on several subjective dimensions: For example, red-yellow transition produces a qualitative change in hue that is accompanied by an increase in brightness and by a decrease in saturation. Similar relations most likely exist between a stimulus and a neural response and between a neural response and sensation.
- e. Furthermore, metric of sensation (and overt response) may differ from that of a neural response. Also, there does not seem to be any parametric work done on the relationship between metric of a stimulus and of a neural response. Theoretical models and methods for appropriately handling these problems still have to be developed (Baird, 1997).

Resolution of these issues would significantly promote research in inner psychophysics by making use of advantages brought about when consolidating the behavioral and neurobiological approaches. In the remainder, we outline the major findings concerning the relations that exist between the stimulus magnitude, neural activation, and sensation/overt response.

The relationships between stimulus, neural activation, and sensation

Sensory magnitude

Most research conducted to date by using conventional neuroimaging modalities (mainly, EEG) has been done on objective threshold determination (e.g., objective audiometry). Apart from early single-cell data, there are very few, if any, parametric studies available on changes in neurophysiological measures as a change along a stimulus dimension extends beyond threshold. The latter kind of work may be referred to as *neurophysiological scaling*. For the more recently introduced modalities (e.g., fMRI), such data does not exist at all. The functional relationships between sensation and neural activation conditional upon the stimulus change are also unknown.

Stimulus magnitude-neural response. Neurophysiological data that utilize event-related or evoked potentials, ERP/EP, recorded in EEG (and most likely, in MEG) as indices of sensory processing, shows that increasing the stimulus intensity generally produces a concomitant increase in the amplitude of ERP components and a reduction in their latency. This holds for the components that are presumably generated in modality-specific cortices; for the components originating in association areas, smaller increases or even decreases are typically observed. For example, increasing the stimulus (flash) intensity enhances the amplitude of transient visual evoked potentials, VEPs, until a plateau is reached (Armington, 1974; Carrillo-de-la-Pena et al., 1999). The latencies of all the VEP components are also affected by changes in flash intensity, with latencies becoming shorter as the intensity increases (Cobb & Dawson, 1960). Pattern VEPs are dependent on stimulus luminance or brightness as well (Arden et al., 1977).

With both visual and auditory modalities, Covington and Polich (1996) find that increases in stimulus intensity produce increases in P300 amplitude and decreases in peak latency. Somewhat weaker stimulus intensity effects are also observed for the N100, P200, and N200 components of VEPs and auditory EPs, AEPs. Both in monkey and in humans, AEPs exhibit a substantial augmentation at frontal, parietal and central sites with increasing tone intensity, and they decrease (or only slightly increase) at temporal sites (e.g., Pineda, Holmes, & Foote, 1991). Some components of brainstem auditory evoked potential (BAEP, with very small amplitudes, below 1 μ V, all together with the latencies up to 10 msec; Jewett, Romano, & Williston, 1970) also appear to be sensitive to a change in the sound intensity (clicks of 80 versus 90 dB). With somesthesia, Gerber and Meinck (2000) report that for the components of somatosensory EP, SEP, below 30 msec, the latencies significantly decline and the amplitudes increase with subsequent saturation. In components beyond 30 msec, the latencies decrease linearly while

amplitudes change non-uniformly. In pain processing, the peak-to-peak amplitude of SEP N150/P250 component increases with intensity of electrical noxious stimulation (e.g., Daum et al., 1995).

Although the neurophysiological studies usually lack reports on the sensory magnitudes associated with the changes in the stimulus intensity and in the evoked potentials, the stimulus variations typically used to elicit a change in neural activation are well above threshold, suggesting that a concomitant change in sensation is present. Because the effects of stimulus intensity on neural activation are robust and site-specific, they should most likely occur also when measured with other functional imaging modalities (e.g., fMRI).

Neural response-sensory magnitude. Very limited evidence exists on the core issue of inner psychophysics, i.e., how the level of neural activation is related to sensory magnitudes. However, here, again, often a monotonic relation is reported. Many studies on this topic come from pain research. Investigating an analgesic effect of nitrous oxide inhalation on vertex ERPs and tooth-pulp pain report elicited by electrical stimulation, Benedetti et al. (1982) found that both ERP amplitude and pain report significantly decreased as dosage increased. In a biofeedback learning paradigm with electrical noxious stimuli, Miltner, Larbig, and Braun (1988) reported that intentionally increasing or decreasing the amplitude of SEP N150/P250 component is associated with a stronger or weaker perceived pain, respectively. High correlations have been also found between pain ratings and the amplitudes of pain-related SEPs (Bromm, 1989; Chudler & Dong, 1983). Derbyshire et al. (1997) conducted a PET study of pain perception as a function of thermal intensity (four levels induced by a CO₂ laser: warm, just painful, mildly and moderately painful). Depending on brain region, both positive and negative correlation of regional cerebral blood flow, rCBF, with stimulus intensity as well as both rCBF increases and decreases with increasing pain ratings were observed. Bloch-Salisbury, Harver, and Squires (1998) studied respiratory ERPs elicited by different levels of inspiratory flow-resistive loads during breathing. They found that like with visual and auditory stimulation, both the latency and amplitude of the late ERP components (P200, N200, and P300) varied systematically as a function of stimulus magnitude, which was quantified both physically and by subjective estimations (as sub-, near-threshold, and near-occlusion).

As with neurophysiological work cited, all these studies lack any parametric examination of the nature of the functional relationship between neural activation and the sensory magnitude.

In psychophysics, overt (behavioral) responses are used to infer the underlying sensory events. Neural activation reflects the overt response-related processes in addition to the solely sensory processing.

Performance (overt response)

The relation between characteristics of a neural and an overt response has been moderately investigated. Beside the ERP methodology, a major EEG/MEG measure considered relevant, especially, for analyzing the speed of response, is lateralized readiness potential, LRP (e.g., Leuthold, Sommer, & Ulrich, 1996). The readiness potential is a slow cortical negativity (up to 10 μ V) arising over motor cortex 1-0.5 sec prior to voluntary movements and abruptly dropping down as their execution begins. Recently, research has also begun on neural predictors of the accuracy of performance.

Speed of response (reaction time, RT). The variability in the timing of overt response is supposed to arise from problems at the stimulus-evaluation (e.g., McCarthy & Donchin, 1981) and response-selection stages (e.g., Coles, 1989; see also Kotchoubey, 1998; Verleger, 1997). For

the former effects, the latency of P300 component of the ERP (with accuracy instructions) and for the latter, latency, amplitude, and sign (for bimanual reactions) of the LPR are presumably indicative (Regan, 1993). In general, RT delays are correlated with the delays in the P300 and in the LPR peak (cf. Kotchoubey, 1998). Either negative or positive sign of the LPR allows one to differentiate between the preparation of correct or incorrect responses.

Accuracy. Neural correlates of accuracy found so far are mainly confined to the internal monitoring of errors in overt responses. For example, it has been argued (e.g., Gratton et al., 1988) that positive LPR on correct trials may indicate a response conflict, when a wrong response is prepared and subsequently suppressed by a subject in favor of executing a correct one. For incorrect choice reactions, Falkenstein et al. (e.g., 2000) describe a negative (Ne) and a later positive (Pe) ERP deflection presumably related to error processing.

The present overview suggests the existence of substantial gaps in our knowledge about the functional links relating the stimulus, the neural response to it, and the sensory magnitude. To bridge these gaps, a simultaneous monitoring of neural activation and behavioral responses conditional upon the stimulus change is required.

Conclusion

Current neuroimaging techniques provide one with a powerful means to study brain function. Although in modern neuroscience, there is no agreement achieved as to which aspects of neural activity most appropriately mirror changes in the stimulus magnitude, some progress has been made. With EEG/MEG, possible candidates are the amplitude and latency of distinct components of event-related brain potentials. Much more limited evidence exists on how the neural activity conditional upon the stimulus relates to the sensory (experienced) magnitude. Systematic parametric research along these lines has yet to be done upon resolution of several important technical and theoretical issues. This can be achieved by a combined effort made by neurophysiology (*neurophysiological scaling*), inner and sensory psychophysics.

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