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A neurocognitive model for short-term sensory and motor preparatory activity in humans

Carlos M. Gómez^{*}, Encarna Vaquero, Manuel Vázquez-Marrufo

Universidad de Sevilla

The purpose of this review is to present information from different experiments that supports the proposal that brain systems are able to predict, in a short-term interval, certain characteristics about the next incoming stimuli. This ability allows the subject to be ready for the stimuli and be more efficient in completing the required task. Evidence is presented from different sensory-motor experiments, such as the central cueing Posner paradigm; Contingent Negative Variation (E1-E2), spectral modulation during expectancy and Lateralized Readiness Potential during the first-order sequential effect. Some cases from motor experiments are also presented, such as express saccades, the manual gap paradigm and ocular smooth pursuit movements. All these data support a neurocognitive model that can be related to neuroanatomical structures whose connections have been well-established. In the final section, a possible algorithm that explains the selection of a preparatory set among the alternatives is discussed.

The aim of attention and its motor counterpart, intention of movement, is to bias the selection of relevant stimuli and appropriate responses to the evaluation of context that the subject makes at a given moment. Stimulus saliency and low threshold responses due to implicitly consolidated S-R habits are certainly a way to partially overcome this huge task. However, on new and open tasks these mechanisms would not be able to produce an adequate selection of stimuli and responses, given the non-consolidated habits and the similar energetic values of different stimuli. Preparatory activity could certainly bias the selection of stimuli and appropriate action.

A few examples will be presented in order to show that the brain is able to interpret the predictive value of a signal and, consequently, prepare the sensory and motor circuits that are going to be needed to perform the task quickly and accurately.

^{*} Correspondencia: Dr. Carlos M. Gómez. Dpto. Psicología Experimental. Facultad de Psicología. C/ Camilo José Cela s/n. Sevilla 41018. España. Tfno: 34-954557800. Fax: 34-954551784. E-mail: cgomez@us.es

SENSORY-MOTOR EVIDENCE

The contingent negative variation (CNV).

In a situation of expectancy induced by a warning stimulus (S1) providing pertinent information about the arrival of a second stimulus (S2, the so-called imperative stimulus), the preparation for S2 induced by the warning generates a change in the cortical activity, which constitutes the CNV (Walter et al. 1964; Rockstroh et al. 1982).

The CNV comprises at least two different phases: an early phase related to stimulus orientation, and a late phase related to preparation for the motor response (Loveless and Sanford, 1974). Some reports suggest the participation of sites responsible for sensory processing in the genesis of CNV (Brunia, 1999; Gómez et al. 2001, 2003). It has been proposed that the S1 acts as a warning stimulus that activates areas needed for the subsequent processing of the S2 stimulus (Brunia, 1999). How task-specific the cortical activation is during the preparatory period, and how it influences the subsequent imperative stimulus, is a subject of much debate and is currently under investigation (i.e. Frith, 2001; Gómez et al. 2001, 2003).

Using directional central cues, two studies have shown slow waves that could represent the pre-activation of sensory cortices, suggesting that the CNV could have a sensory component (Deecke et al. 1984, Harter et al. 1989). Electrophysiological recordings of single neurons in animals and fMRI studies in humans (Requin et al. 1990, Luck et al. 1997, Kastner et al. 1999, Lee et al. 1999) support the activation of the frontal, striate and extra-striate cortices during preparatory periods while visual stimulation is delivered. Based on these observations, one could postulate that the neural preparatory activity in primary motor (Cui et al. 2000, Gómez et al. 2003) and posterior sites (Gómez et al. 2001, 2003) anticipates the activation of these same areas, which are needed for the actual processing of the imperative stimulus.

One clear example of this appears in an experiment where a central light warns of the presentation of a peripheral light. In this experiment, in addition to the activation of the prefrontal and cingulate cortices, there is an activation of the primary motor cortex contra-lateral to the hand to be used and from different visual areas, indicating that the areas that are needed for the processing of the next stimuli are pre-activated (Gómez et al. 2003).

In fact, this pattern of brain activation could explain the cost-benefit pattern of the Posner-type paradigm (Posner & Cohen, 1984). In the Posner-type central-cue experiment, the cueing of a probable location for the imperative stimulus produces a faster response when the cue is valid compared to an invalid or neutral cue. This behavioral outcome implies that some neural activation, probably the activation of the cued motor and sensory cortices, must occur during the preparatory period, in order to allow a faster reaction time (RT) when comparing valid and invalid or neutral conditions. Recently, in a Posner-type experiment (Gómez et al. 2004a) where a directional central arrow indicates in which ear an imperative stimulus will

appear (validity of the cue 84%), the activation of the primary auditory cortex and the corresponding primary motor cortex was observed by analyzing the contingent magnetic variation (CMV). This pattern of neural activation could explain the cost-benefit pattern of the RTs observed in Posner-type central cue experiments: benefit when the central arrow allows the activation of the cortex that would receive the stimulus and produce the response, and cost when the incorrect sensory and motor cortices are activated and a reorientation of attention must occur.

The presence of a task-specific cortical network has also been detected in the differential topographies of the negative slow waves registered during the retrieval of different items during a memory task (Rösler et al. 1995). In the review carried out by Brunia (2001), the ability of cortically generated slow negative potentials to index the preparatory processes dealing with selection is pointed out. The functionality of these negativities is based on the proposal that they are a consequence of the tonic depolarization of apical dendrites in the cortex, which would allow a state of elevated excitability so the firing threshold can be reached (Rockstroh et al. 1982).

Event related desynchronization during the expectancy period.

The CNV tonic activity is not the only neural signal that can be detected in the preparatory periods prior to the appearance of the target stimulus. In fact, analysis using ERPs disregards possible modulations of the different spectral components present in the EEG (alpha, beta, gamma, etc.). Various approaches, such as Fourier-fast transform (Gómez et al. 1998), event-related desynchronisation (ERD) (Pfurtscheller and Lopes da Silva, 1999), or temporal spectral evolution (TSE) (Salmelin, R. and Hari, R. 1994, Vázquez et al. 2001), have been used to evaluate the modulations of the spectral bands related to attention, working memory and other processes. ERD is a technique that consists of the following three steps: (1) the EEG epochs are digitally band-pass-filtered in the desired range (for instance 8-12 Hz in the case of alpha) (2) the signal resulting from filtering is squared and, finally, (3) averaged separately for each experimental condition. Use of ERD has shown a modulation in alpha and beta bands on a variety of tasks related to the attentional and intentional preparation for the stimulus. For instance, ERD in the alpha range has been found in the motor cortex during preparation for movement (Pfurtscheller and Lopes da Silva, 1999) and during expectancy of a visual feedback stimulus (Bastiaansen et al. 1999, Bastiaansen and Brunia, 2001). A generalized reduction of the spectral power of the EEG during expectancy situations has been described, indicating that changes in oscillatory activity during expectancy could occur in a cortically distributed manner (Gómez et al. 2004b). Alpha increase has also been obtained during preparatory periods in areas that should be deactivated for a correct performance of the task (Worden et al. 2000, Fu et al. 2001) and prior to an imperative stimulus on a category judgment task (Klimesch, 1992). The latter has been explained as the selective inactivation of some brain areas (Pfurtscheller and Lopes da Silva, 1999).

Brain oscillatory activity will result from synchronicity of the activity in more-or-less distributed networks that would include at least cortico-cortical and thalamic-cortical networks. Underlying these oscillations would be not only the dynamic interaction between distributed groups of neurons, but also intrinsic membrane properties and the influence of neurotransmitter systems (Lopes da Silva, 1991; Singer and Gray, 1995). Given the different topographies of CNV and ERD, a different mechanism for the proposed tonic depolarization of the apical dendrites must be proposed in order to account for the predictive ERD. In fact, the independence of alpha ERD and CNV has already been described (Filipovic et al. 2001). One possibility arises from the influence of locus coeruleus on cortical systems during expectancy situations. A broad reduction of spectral power on the EEG after consumption of caffeine (a noradrenergic agonist that increases the subject's vigilance) has been described (Gilbert et al. 2000; Siepmann and Kirsch, 2002), just as it has been described in stimulus-induced expectancy (Gómez et al. 2004b). The role of increasing the signal-to-noise ratio of the relevant stimulus has been proposed for the noradrenergic system. These results make it possible to speculate that the locus coeruleus (Aston-Jones et al. 1999) and/or other noradrenergic nuclei could facilitate the attentive processing of cognitive information by reducing the EEG power in the late phase of the expectancy period.

The first-order sequential effect.

One particular case where the specific preparation for movement has been clearly demonstrated is in the analysis of sequential responses to a series of random targets during discrimination tasks. A response-time dependent on the sequence of the previous stimuli has been exhaustively proven. Among the most conspicuous effects are the first-order effects due to the preceding stimulus, whether they are equal to (repetition) or different from (alternated) the preceding stimulus (Soetens, 1997). These first-order effects are dependent on the time elapsed from the current stimulus to the preceding response: the so-called response stimulus interval (RSI). The most common effect is that, for short RSI (less than 500 ms), the reaction time is shorter for repeated stimuli than for alternate stimuli. When the RSI exceeds 500 ms, the repetition effect decreases, and in some cases it can become an alternating effect (Bertelson and Renkin, 1966). This differential effect for short and long RSI has been attributed to the operation of two different mechanisms (Kirby, 1980; Soetens, 1997). The repetition effect during short RSI could be due to an automatic facilitation. The alternating effect that appears during long RSI can be explained by a subjective bias about the probability of which stimulus will be next. The process is controlled by an increased subjective expectancy to the stimulus opposite to that previously presented. This is similar to the so-called "gambler's fallacy", where subjects believe that conditioned probability exists between an event and the previous one, whereas they are actually totally independent.

One Event Related Potentials (ERPs) study tends to support the view that subjects do prepare the response alternate to the one previously executed. In that particular experiment, a tone of different frequency signaled the response hand. The lateralized readiness response (LRP component) showed that subjects prepared the responses corresponding to the hand that had not been used in the previous stimulus (Leuthold & Sommer, 1993); that is, they prepared the alternate response. If the arriving stimulus is the same as that previously presented, a correction of the movement occurs that is reflected as a change of trend in the LRP component. A similar LRP behavior has been obtained when visual stimuli, rather than auditory tones, are used (Gómez et al. 2004c).

MOTOR EVIDENCE

The express saccades and the gap effect.

In express saccade experiments (an experimental condition where there is a temporal gap of around 200 ms between the switching off of the central fixation and the switching on of the peripheral target), the latencies of saccadic eye movements are reduced in gap conditions with respect to non-gap conditions (Fischer & Weber, 1993). The saccadic latencies are measured as the time difference between the appearance of the target and the initiation of movement. One particularly interesting result appears from the following: the final eye position is a weighted average (as a function of time from the switching on of the peripheral target) between the predicted eye position and the actual location of the incoming stimulus (Delinte et al. 2002). This result suggests that the parameters of the saccade are predicted in advance of the arrival of the target stimulus, and that these parameters can be modified by the current stimulus. The physiological proposal to explain the reduced RTs suggests that during the gap period the subject guesses the position of the future target, which would produce the activation of the retinotopic motor map in the superior colliculus. If the stimulus arrives in the predicted position, a considerable (around 50 ms) reduction of the RTs of saccades would occur.

A phenomenon similar to the express-saccades has been described in skeletal movements, using the same experimental paradigm, with a temporal gap of around 200 ms between the extinction of fixation and the target. In this case, a reduction of response times (RTs) has also been described (Gómez et al. 1998). Clear signs of motor cortex activation in the preparatory periods have been described during this kind of paradigm (Csibra et al. 1997, Gómez et al. 2001). This motor pre-activation could be the basis of anticipations, given that both eye and manual responses produce more anticipations in gap conditions than in non-gap conditions (Gómez et al. 1996, 1998). The most interesting neural effect of interposing a gap between the switching off of the warning central light and the switching on of the peripheral light corresponds to an acceleration of the activity in the motor cortex, measured as a lateralized negativity recorded in the electrodes overlying the motor cortex (Gómez et al. 2002).

Two corollary consequences emerge from these experiments (i) The eye movement produces many more anticipations during the gap effect than the manual movements do, indicating that the threshold for responses is lower in the eye movement system than in the skeletal system (Delinte et al. 2002; Gómez et al. 1998), and (ii) responses can arrive to threshold with only the preparation signal producing anticipations. The last point is dramatically observed during eye saccades in gap paradigms with fixed direction and location of the target. In this case a high percentage of saccades occurs during the gap period before the target appears (Gómez et al. 1994).

Smooth pursuit movements.

The smooth pursuit movements make it possible to keep the object of interest in the retina when the object moves at a slow angular velocity. The typical angular velocity in such experiments is around 20 to 40 deg/s. If the eye movement does not reach the same angular velocity as the object, it cannot be foveated, and its image blurs. Most people need the presence of a moving target in order to perform smooth pursuit movements. However, if the appearance of the moving target is predictable in terms of its timing, speed and direction, an anticipatory smooth pursuit can occur without the physical presence of the stimulus.

The ability to predict the movement parameters of the object is obtained by a few repetitions of cue and moving target, allowing the cue to acquire predictive properties about the timing and velocity of the moving visual stimulus. It has been proposed that this process depends on the build up of a short-term store of target velocity (which makes it possible to generate the eye velocity signal) combined with a timing mechanism that indicates the time of stimulus initiation.

The anticipatory capabilities of the system do not rely exclusively on prior target movements, but they can be produced by symbolic information. Symbolic cues can be used to volitionally control the velocity and the direction of the predictive smooth movement. This predictive movement is considered to be ballistic and pre-programmed, and it receives little influence from visual feedback. Moreover, recently it has been shown that anticipatory smooth pursuit can be volitionally stopped (Jarrett and Barnes, 2003). From data provided by functional magnetic resonance imaging, it has been proposed that the dorsomedial frontal cortex, including the supplementary motor area and the supplementary eye fields, would be able to trigger the predictive smooth pursuit through the activation of the frontal eye fields that would activate the common pathway for smooth pursuit via the cerebellum (Schnid et al. 2001).

A general mechanism for prediction and anticipation in the brain.

From these few selected examples, it can be proposed that the brain is able to anticipate some characteristic of the next incoming stimuli. This preparation can range from preparing the hand to respond (CNV, sequential order effect and gap paradigm), the sensory cortex where the stimulus is

expected to appear (CNV and CMV), the suppression of specific rhythms in specific cortices (ERD), the full specification of detailed parameters (amplitude, direction, timing) of the intended movement (anticipatory smooth pursuit and express saccades), or the expected stimuli (visual and auditory cortex activation indexed in the CNV and CMV experiments respectively).

Is it possible to propose a plausible general mechanism for how the brain is able to pre-activate the areas that it supposes are going to be needed for processing and responding to next stimuli? The experiments considered above (Schrnid et al. 2001, Gómez et al. 2003) point to the frontal cortex as the starting point for creating a preparatory set. More specifically, the CNV and the anticipatory “smooth pursuit movement” experiments suggest that the frontomedial cortex, basically the supplementary motor area, is the initiator of the readiness process. In fact, the earliest volitionally-induced activity that appears during the so-called *Bereitschaftspotential* (BP) also has its origin in this area, as has been proposed by Deecke and Cui (1999). They proposed that the BP is in fact composed of three subsequent negativities related to motor preparation and execution. The first is an initial phase called BP1, which possibly originates in the supplementary motor area (SMA) and cingulate motor areas (CMA). Both areas will participate in the organization of sequential movements and bimanual coordination. The BP2 and BP3 may originate in the primary motor cortex (M1) and index executive processes in the contralateral M1. Furthermore, the fMRI, using a paradigm similar to that used for obtaining CNV, supports previous findings based on electrophysiological techniques, showing activation of the Anterior Cingulate Cortex (ACC) and SMA in the preparatory periods and of M1 in the executive response (Lee et al. 1999). The posterior cingulated cortex could be one of the sources in the preparation of a behavioral set, particularly in the Posner-type paradigm (Gómez et al. 2004a). The important role of the medial and superior frontal cortices in the endogenously generated movement has been recently stressed by Lau et al. (2004), showing an increase in activity in the pre-SMA area. When attending to the intention to move, this activity was highly correlated with the right lateral prefrontal cortex.

Therefore, the sequence of activations obtained suggests that SMA and ACC start the process of preparing for action and perception. These areas might be able to recruit the specific sensory and motor cortex activation (Gómez et al. 2001, 2003, 2004a) needed for the sensory and motor processing of the imperative stimulus (Lee et al. 1999, Kastner et al. 1999). The SMA area presents efferent connectivity to posterior sensory association cortex and to primary motor areas (Künzle, 1978). The function of the dorsolateral prefrontal and middle frontal cortices (PFC/MFC) could be to sustain activation in the sensory and motor cortices. The mechanism for this would lie in reciprocal interactions between PFC/MFC with both M1 and posterior visual areas, in a way similar to what occurs in working memory experiments such as delayed matching-to-sample tasks in monkeys (Fuster, 2000). The SMA presents short connection fibers that functionally link SMA and ACC with the dorsolateral PFC, allowing the PFC to participate in keeping the preparation process active (Bates and Goldman-Rakic, 1993). It

must be stated that the previously described connections are found in different kinds of animals, and it is always possible that they do not exist in humans. Furthermore, the functional efficacy of this connection is difficult to test. In this sense, the previous connectivity argument must be understood as a supportive claim.

Simultaneous to the preparation indexed by slow negative potentials such as the CNV, there is a generalized reduction in the EEG power during expectancy situations (Gómez et al. 2004b). In a similar way, a broad reduction of spectral power in the EEG after consumption of caffeine (a noradrenergic agonist that increases the subject's vigilance) has been described (Gilbert et al. 2000; Siepmann and Kirsch, 2002). The role of increasing the signal-to-noise ratio of the relevant stimulus has been proposed for the noradrenergic system. In fact it has been shown that noradrenaline can produce a reduction in spontaneous activity, while producing an increase in evoked activity. These results allow one to speculate that the locus coeruleus (Aston-Jones et al. 1999) and/or other noradrenergic nuclei might facilitate the attentive processing of cognitive information by reducing the EEG power in the late phase of the expectancy period. The locus coeruleus present inputs arriving directly from the dorsal prefrontal cortex (Arnsten and Goldman-Rakic, 1984), which is also directly connected with the SMA area. Moreover, the locus coeruleus also receives inputs from the anterior cingulate cortex (Buchanan et al. 1994). It must also be pointed out that plasma noradrenaline concentration is positively correlated with CNV amplitude, suggesting that the noradrenergic system including locus coeruleus could affect the attentive processing in its two operational modes: decreasing brain oscillations and lowering the neural threshold as indexed by CNV (Timsit et al. 1987).

In this sense, the reduction of the EEG power would facilitate the attentive processing, by eliminating oscillations that would increase the neural noise. Simultaneously, the tonic depolarization of apical dendrites, as indexed by the CNV, would reduce the threshold of neurons for the incoming stimulus and trigger a response.

In addition to the noradrenergic system, the cholinergic inputs from the basal forebrain to the cortex play an important role in controlling arousal and attentive processing in the brain (Sarter and Bruno, 2000). The cortex itself can regulate the activity of the basal forebrain through feedback connections. In fact, nicotinic receptors have already shown a modulatory effect of CNV; i.e., nicotinic administration produced an increase in the CNV amplitude (Michel et al. 1988). Then the combined activity of noradrenergic and cholinergic inputs to the cortex would provide the needed cortical excitability to establish a selective activation probably based in corticothalamic reciprocal interaction, given the lack of cortical specificity of the brain stem and basal forebrain to the cortex (Sarter and Bruno, 2000).

However, the previous description occurs at a systemic level, and it would be top-down driven from medial cortices (SMA and ACC, but also posterior cingulate cortex). Some kind of more detailed mechanism at a cellular level must account for the precise selective motor anticipation that

occurs; i.e., in the saccade express and the anticipatory smooth pursuit experiments, where prediction occurs at the level of positional, timing and kinematic properties of the movements. The key algorithm for such a selective process must be some kind of “higher influential activity”, also termed as the “competition or winner-take-all mechanism”. It must be stated that as all potential action and stimuli are potentially adaptive for the whole individual, the term competition must be understood basically in its selective meaning. However, the mechanism of selection must occur at various levels, given the impossibility of a generalized lateral inhibition process that would highlight a specific spatial location on a saliency map. This kind of selective mechanism has extensive behavioral (Gómez et al. 1992, 1995), single cell (Desimone and Duncan, 1995) and systemic data supporting it (Kastner and Ungerleider, 2001), but there is no complete and integrated picture of how it works, and it probably includes extensive lateral inhibition between the different spatial and object representations. Of course, the bias produced by the preparatory set would highly influence the outcome of the selective process by increasing the probability of a given neural representation to overcome the activity of other neural representations.

CONCLUSION

The different experimental paradigms described here make it possible to propose that experimental cues, as well as spontaneous guesses about the characteristics of the next stimulus, induce the recruitment of the brain circuits that are needed to process the expected stimuli. The SMA and the ACC would be important areas to include endogenous expectancy in the stream of neural processing.

RESUMEN

Un modelo neurocognitivo de la actividad sensoriomotora de carácter preparatorio en humanos. La propuesta de esta revisión es presentar información, obtenida en diferentes experimentos, que apoyan la propuesta de que los sistemas cerebrales son capaces de predecir, en intervalos cortos de tiempos, ciertas características acerca del siguiente estímulo. Esta capacidad permite a los sujetos estar preparados para los estímulos y ser más eficientes en completar la tarea requerida. En este sentido presentamos evidencia proveniente de diferentes experimentos sensoriomotores, como el paradigma de clave central de Posner; la variación contingente negativa (E1-E2); la modulación espectral durante expectativa y el potencial lateralizado de preparación (efecto secuencial de primer orden). Igualmente se presentan algunos paradigmas motores tales como las sacadas express, el paradigma de “gap” manual y los movimientos de seguimiento ocular. Todos estos datos apoyan un modelo neurocognitivo que puede ser relacionado con estructuras neuroanatómicas cuya conexión ha sido bien establecida. En la sección final se presenta un posible algoritmo que podría explicar la selección de actividad preparatoria entre distintas alternativas.

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